FIELDIANA

Zoology

A MULTIVARIATE STUDY OF THE FAMILY MOLOSSIDAE
(MAMMALIA, CHIROPTERA):
MORPHOLOGY, ECOLOGY, EVOLUTION

PATRICIA WARING FREEMAN

A MULTIVARIATE STUDY OF THE FAMILY MOLOSSIDAE (MAMMALIA, CHIROPTERA): MORPHOLOGY, ECOLOGY, EVOLUTION

FIELDIANA
Zoology

Published by Field Museum of Natural History

New Series, No. 7

A MULTIVARIATE STUDY OF THE FAMILY MOLOSSIDAE (MAMMALIA, CHIROPTERA): MORPHOLOGY, ECOLOGY, EVOLUTION

PATRICIA WARING FREEMAN

Assistant Curator and Head
Division of Mammals
Department of Zoology
Field Museum of Natural History

CONTENTS

LIST OF ILLUSTRATIONS

LIST OF TABLES

ACKNOWLEDGMENTS

This study was originally done in partial fulfillment of the requirements for the degree of Doctor of Philosophy in biology in the graduate school of the University of New Mexico in May, 1977. In the present publication certain sections have been revised and a synonymy and key to the genera have been added as appendices.

The following institutions and their curators kindly supplied me with specimens:

AMNH	The American Museum of Natural History, Karl F. Koopman, Curator
BJH	Private collection of Bruce J. Hayward, Department of Biology, Western New Mexico University
BM	British Museum (Natural History), John E. Hill, Curator
FMNH	Field Museum of Natural History, Luis de la Torre, Curator
LSU	Louisiana State University Museum of Zoology, the late George H. Lowery, Curator
ROM	Royal Ontario Museum, Randolph L. Peterson, Curator; and Judith L. Eger, Curatorial Assistant
TCWC	Texas Co-operative Wildlife Collection, Texas A&M University, David Schmidly, Curator
UA	University of Arizona, G. Lendell Cockrum, Curator

MSB   Museum of Southwestern Biology, University of New Mexico,
           James S. Findley, Curator
USNM   United States National Museum, Charles O. Handley, Curator; and
           Don E. Wilson, Chief, Section of Mammals, National Fish and
           Wildlife Laboratories
WNMU   Western New Mexico University, Bruce J. Hayward, Curator

INTRODUCTION

Bats of the family Molossidae are as distinctive as they are elusive. Free-tailed
bats are thought to be the swiftest of all bats and tend to fly well above the
canopy and out of human reach. Because of such habits, specimens of some
species of molossids are not abundant and taxonomic and ecologic knowledge
of the family is not extensive.

Molossids are distinctive not only because of their vespertilionoid shoulder,
which is at its highest development, narrow wing, and tail, which extends well
beyond the posterior border of the uropatagium; but also because of their
unique faces, their short, velvety fur, and their tough, leathery skin (Vaughan,
1972, pp. 111–113).

The first molossid to receive a scientific name was *Vespertilio Molossus* Pallas,
1766, from the New World, and so named because of its resemblance to a black
mastiff from the Greek province of Molossis. This dog-faced appearance is
common to several genera within the family. Actually, *Vespertilio Molossus* in-
cluded specimens that are now called *Tadarida macrotis* and *Molossus molossus*
(Husson, 1962). Many members of the family have deeply wrinkled lips and
large ears that project anteriorly and laterally to look like a wide-brimmed hat;
others have widely separated, smaller, and more pointed ears and no wrinkles
on the lips. Most of the species have unusual spoon-shaped hairs on the muzzle
and toes, as well as a gland on the chest which emits an odor unique to molos-
sids.

Molossids are insectivorous and live in tropical and temperate parts of the
world. More than half the species are members of the genus *Tadarida*, which
historically includes four subgenera: *Chaerephon*, *Mops*, *Mormopterus*, and
Tadarida. The remaining species are spread among 11 other genera. Species of
Tadarida (*sensu lato*) are found in both hemispheres, but each region has its own
endemic molossid genera: *Molossus*, *Eumops*, *Promops*, *Cynomops*, *Molossops*,
and *Neoplatymops* in the New World; and *Otomops*, *Myopterus*, *Platymops*,
Sauromys, and *Cheiromeles* in the Old World.

The purpose of my study is to examine as many species of the family Molos-
sidae as possible and to determine, with the aid of numerical methods, what
natural groups exist within the family. Sneath & Sokal (1973) discuss the
methods and reasons for this kind of analysis. A natural group of organisms as
here defined is one in which its members share a close phenetic relationship.
Phenetic relationship is defined as "similarity (resemblance) based on a set of
phenotypic characteristics of the objects or organisms under study," (Sneath &
Sokal, 1973, p. 29), and is distinct in definition from phylogenetic relationship.
However, I have used phenetic relationships to help estimate phylogenetic
ones. I think that the estimation of the evolutionary relationships from phenet-
ics is best observed when size of the organism is not a factor, and for this
reason, I place much emphasis on the shape analyses in my study (for a discus-

sion, see Sneath & Sokal, 1973, pp. 168–178). Analysis with size included can be very important in the estimation of ecological relationships.

A natural group of bats in the family Molossidae includes individuals of a certain shape category and can be distinguished from individuals of a different shape category. I think each shape category or group indicates a certain way of life. Often, these natural shape groups correspond with classical genera or subgenera and are described in terms of those taxonomic names. Here, I examine the family Molossidae phenetically, determine how many natural shape groups have evolved within it, predict the resulting diverse ways of life, and estimate the evolutionary relationships among the species and groups. A few of the characters can be graded as to their primitive-derived nature and accompany the evolution discussion. The analyses used were designed not so much to distinguish one species from another, but to detect underlying morphological trends.

No intensive world-wide study of molossids has been attempted. Miller (1907) reviewed the nominal genera known at the beginning of this century and provided morphological descriptions which are precise and meticulous. Early reviews of genera are by Miller (1913) of *Molossus*, by Shamel (1931) of New World *Tadarida*, and by Sanborn (1932) of *Eumops*. All three studies were done with far less material than is available today. Recently, Eger (1977) has examined more closely the genus *Eumops* and rigorously defined the species in that genus.

Prominent taxonomic studies of molossids in the Old World are those by Hill (1961) of Indo-Australian *Tadarida* (*sensu lato*) and by Hayman & Hill (1971). The latter authors offer keys and compilations of information on all African Chiroptera. Koopman (1975) has reviewed the bats of the Sudan and provided much data about Old World Molossids.

Important systematic papers on individual species of molossids are by Peterson (1965, 1967, 1969, 1971a,b, 1972, 1974), who has not only examined many specimens in museums, but has also spent much time in the field collecting the bats and gathering data on their habits and habitat. Recently, Koopman (1978) has added significant zoogeographic and systematic notes on Peruvian molossids. Vaughan (1959, 1966) has studied the wing musculature and flight characteristics of some molossids, and Pye (1966) and Simmons et al. (1978) have done much to reveal the echolocating abilities in molossids.

The following outline is the current status of species of Molossidae examined in this study (for details see Appendix B):

Tadarida Rafinesque, 1814
  (*Tadarida*) Rafinesque, 1814
    aegyptiaca E. Geoffroy, 1818
    africana Dobson, 1876
    ansorgei Thomas, 1913
    aurispinosa Peale, 1848
    australis Gray, 1838
    brasiliensis I. Geof. St. Hilaire, 1824
    femorosacca Merriam, 1889
    fulminans Thomas, 1903
    kuboriensis McKean & Calaby, 1968
    laticaudata Geoffroy, 1835
    lobata Thomas, 1891

    macrotis Gray, 1839
    teniotis Rafinesque, 1814

Tadarida
  (*Chaerephon*) Dobson, 1874
    aloysiisabaudiae Festa, 1907
    bemmelini Jentink, 1879
    bivittata Heuglin, 1861
    chapini J. A. Allen, 1917
    jobensis Miller, 1902
    johorensis Dobson, 1873
    major Trouessart, 1887
    nigeriae Thomas, 1913
    plicata Buchanan, 1800

pumila Cretzschmar, 1826
russata J. A. Allen, 1917

Tadarida
  (*Mops*) Lesson, 1842
    brachyptera Peters, 1852
    condylura A. Smith, 1833
    congica J. A. Allen, 1917
    demonstrator Thomas, 1913
    leonis Thomas, 1908
    midas Sundevall, 1843
    mops de Blainville, 1840
    nanula J. A. Allen, 1917
    niangarae J. A. Allen, 1917
    niveiventer Cabrera & Ruxton, 1926
    sarasinorum Meyer, 1899
    thersites Thomas, 1903
    trevori J. A. Allen, 1917
Xiphonycteris Dollman, 1911
    spurrelli Dollman, 1911

Tadarida
  (*Mormopterus*) Peters, 1865
    acetabulosus Herman, 1804
    beccarii Peters, 1881
    jugularis Peters, 1865
    kalinowskii Thomas, 1863
    loriae Thomas, 1897
    minutus Miller, 1899
    norfolkensis Gray, 1839
    phrudus Handley, 1956
    planiceps Peters, 1866
Cheiromeles Horsfield, 1824
    parvidens Miller & Hollister, 1921
    torquatus Horsfield, 1824
Cynomops Thomas, 1920
    brachymeles Peters, 1865
    greenhalli Goodwin, 1958
    planirostris Peters, 1865

Eumops Miller, 1906
    auripendulus Shaw, 1800
    bonariensis Peters, 1874
    glaucinus Wagner, 1843
    hansae Sanborn, 1932
    maurus Thomas, 1901
    perotis Schinz, 1821
    underwoodi Goodwin, 1940

Molossops Peters, 1865
    temminckii Peters, 1865

Molossus Geoffroy, 1805
    ater Geoffroy, 1805
    bondae J. A. Allen, 1904
    coibensis J. A. Allen, 1904
    molossus Pallas, 1766
    pretiosus Miller, 1902
    sinaloae J. A. Allen, 1906
    trinitatus Goodwin, 1959

Myopterus E. Geoffroy, 1818
    albatus Thomas, 1915
    whitleyi Scharff, 1900

Neoplatymops Peterson, 1965
    mattogrossensis Vieira, 1942

Otomops Thomas, 1913
    martiensseni Matschie, 1897
    papuensis Lawrence, 1948
    secundus Hayman, 1952
    wroughtoni Thomas, 1913

Platymops Peters, 1878
    setiger Peters, 1878

Promops Gervais, 1855
    centralis Thomas, 1915
    nasutus Spix, 1823

Sauromys Roberts, 1917
    petrophilus Roberts, 1917

MATERIALS AND METHODS

Specimens Examined

As explained earlier, my object was to find as many morphologically distinct forms of molossid bats as possible. I assumed that distinct forms or morphotypes are represented by species rather than subspecies. Of an estimated 82 nominal species in the family (Koopman, 1970), 78 were included in my study. Species named in the literature and left out because of difficulty in locating or getting to the specimens are *Molossops aequatorianus* Cabrera, 1957; *Myopterus daubentoni* Desmarest, 1820 (*M. albatus?*, see Hill, 1969); *Otomops formosus*, Chasen, 1939; *Tadarida* (*Mormopterus*) *doriae* Andersen (see Hill, 1961); and the recently described *Tadarida* (*Chaerephon*) *gallagheri* Harrison, 1975.

I attempted to procure an adult male and female of each species, but because

many species of molossids are rare in collections, I often could obtain only one sex. Sexual dimorphism is common in the family, with the male usually being larger and having more distinctive features than the female. I performed a preliminary test on 155 bats to see if males and females of the same species could be safely grouped to represent one morphotype and to see if questionable species or subspecies could be grouped to represent one species or OTU (operational taxonomic unit, see Sokal & Sneath, 1963). With few exceptions, males and females of the same species were phenetically closer to each other than they were to any other bat in the study and subsequently were treated together. Because the magnitude of variation between several subspecies of *Molossus molossus* was slight, I did not believe that individual treatment of the subspecies was justified. *Molossus coibensis*, another possible subspecies of *M. molossus*, was phenetically similar to *M. bondae* and was left in the analysis. The three Australian *Tadarida* (*Mormopterus*), *T. (M.) loriae*, *T. (M.) planiceps*, and *T. (M.) norfolkensis*, were also kept because the 155-bat study did not put males and females of the same species together. There are 80 OTU's in the final analysis on which all discussion is based. Two OTU's are representatives from the family Vespertilionidae, added for comparative purposes.

The specimens used and their abbreviations, which appear in the tables and figures, are listed below. Each number represents an OTU.

1. *Tadarida* (*Tadarida*) *aegyptiaca aegyptiaca* (T AEGYPA,[1] Tae)
      AMNH 81864 ♂—South Africa: Natal; 16 miles NE Port Shepstone
      AMNH 217023 ♀—Kenya: Eastern Prov.; Sultan Hamud
   Tadarida (*Tadarida*) *aegyptiaca bocagei*
      *USNM 156339 ♂—South Africa: Transvaal; Potchefstroom
2. *Tadarida* (*Tadarida*) *africana* (T AFRICA, Taf)
      BJH 3333 ♂—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
      BJH 3341 ♀—same as ♂
3. *Tadarida* (*Tadarida*) *ansorgei* (T ANSORA, Tan)
      AMNH 48902 ♂—Zaire: Faradje
      AMNH 48904 ♀—same as ♂
4. *Tadarida* (*Tadarida*) *aurispinosa* (T AURISA, Tau)
      TCWC 13897 ♂—Mexico: Tamaulipas; 2 miles W El Abra, Cueva del Abra
      TCWC 13895 ♀—same as ♂
5. *Tadarida* (*Tadarida*) *australis* (T AUSTRA, Tas)
      *AMNH 153414 ?—Australia: Queensland; Birdsville area
      AMNH 220157 ♂—West Australia: Elduna R. H.; 29° 5′ S, 127° 25′ E
      AMNH 220156 ♀—same as ♂
6. *Tadarida* (*Tadarida*) *brasiliensis* (T BRASIA, Tb)
      MSB 13558 ♂—New Mexico: Socorro Co.; 6½ miles W and 2 miles S Socorro
      MSB 13557 ♀—same as ♂

---

[1] Each abbreviation (all capital letters) ending with the letter A represents the average of a male and female specimen.

*An asterisk indicates the specimen was not used in the final analysis containing 80 OTU's.

7. *Tadarida (Tadarida) femorosacca* (T FEMORA, Tfe)
    MSB 26859 ♂—Mexico: Sonora; one-half mile E cemetery of Alamos
    MSB 26860 ♀—same as ♂
8. *Tadarida (Tadarida) fulminans* (T FULMIN, Tfu)
    BM 82.3.134 ♂ type—Madagascar: Fianarantsoa; E Betsileo
9. *Tadarida (Tadarida) kuboriensis* (T KUBORI, Tk)
    AMNH 157434 ♀—Papua: Mt. Dayman (Maneau Range), N slope
10. *Tadarida (Tadarida) laticaudata laticaudata* (T LATICA, Tla)
    AMNH 75526 ♂—Brazil: Roraima; Mt. Roraima, Paulo
    AMNH 75527 ♀—same as ♂
    Tadarida (Tadarida) laticaudata europs
    *AMNH 79514 ♂—Brazil: Rio Negro, Sta. Maria
11. *Tadarida (Tadarida) lobata* (T LOBATA, Tlo)
    BM 70.727 ♂—Kenya: Cherangani Hills; Kaibibich; 1° 10′ N, 35° 22′ E
    ROM 68488 ♀—Kenya: Taita Taveta Dist.; 30 km. SE Voi, Maungu Hill
    *ROM 68090 ♂—same as ROM ♀
12. *Tadarida (Tadarida) macrotis* (T MACROA, Tm)
    MSB 35601 ♂—New Mexico: Los Lunas
    MSB 19223 ♀—New Mexico: Hidalgo Co.; dirt tank N NM79; R19W,
            T34S, Sec.33
13. *Tadarida (Tadarida) teniotis* (T TENIOA, Tt)
    BM 15.10.2.1 ♂—Egypt: Giza; Aburoash
    FMNH 79288 ♀—Egypt: Giza; Abu Rawash
14. *Tadarida (Chaerephon) aloysiisabaudiae* (TC ALOYA, TCa)
    ROM 59231 ♂—W. Uganda: Budongo Forest
    ROM 38380 ♀—W. Uganda: Budongo Forest, near Masindi
15. *Tadarida (Chaerephon) bemmelini* (TC BEMMI, TCbe)
    AMNH 83921 ♂—Tanzania: Mawere
16. *Tadarida (Chaerephon) bivittata* (TC BIVIA, TCbi)
    BJH 3338 ♂—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
    BJH 3337 ♀—same as ♂
17. *Tadarida (Chaerephon) chapini* (TC CHAPI, TCc)
    AMNH 48841 ♂ type—Zaire: Faradje
18. *Tadarida (Chaerephon) jobensis* (TC JOBEN, TCjb)
    AMNH 107804 ♂—Australia: Queensland; Malbon
19. *Tadarida (Chaerephon) johorensis* (TC JOHOR, TCjh)
    BM 73.637 ♀—Malaya: Kelantan; Pulai
20. *Tadarida (Chaerephon) major* (TC MAJOR, TCm)
    AMNH 48838 ♀—Zaire: Faradje
21. *Tadarida (Chaerephon) nigeriae nigeriae* (TC NIGEA, TCni)
    USNM 420092 ♂—Ghana: Subinja; Broug-Ahato Region, Oerived
            Savannah ca. 2 miles E Wenchi; 7° 45′ N, 2° 4′ W
    USNM 421517 ♀—Dahomey: Segbana, Borgou Region; ≃10° 56′ N,
            3° 42′ E
    Tadarida (Chaerephon) nigeriae spillmani
    *AMNH 115944 ♂—Zambia: Balovale
    *AMNH 115947 ♀—same as ♂
22. *Tadarida (Chaerephon) plicata* (TC PLICA, TCpl)
    AMNH 101610 ♂—Java: Cheribon
    AMNH 107955 ♀—Indonesia: Bali; Noesa Penida

23. *Tadarida (Chaerephon) pumila pumila* (TC PUMIA, TCpu)
    BJH 2191 ♂—Kenya: Naivasha; E edge Lake Naivasha
    BJH 2192 ♀—same as ♂
    Tadarida (Chaerephon) pumila gambiana
        *USNM 412176 ♀—Ghana: Volta Region; Bator; 6° 5′ N, 0° 25′ E
    Tadarida (Chaerephon) pumila limbata
        *BJH 3551 ♂—Kenya: 2 miles N Kilifi
        *BJH 3545 ♀—same as ♂
    Tadarida (Chaerephon) pumila hindei
        *WNMU 373 ♂—Kenya: Donyo Sabuk Mts.; 32 miles E Nairobi
    Tadarida (Chaerephon) pumila nigri
        *AMNH 90390 ♂ paratype—Mali: Timbouctou Dist.; Bourem
24. *Tadarida (Chaerephon) russata* (TC RUSSA, TCr)
    AMNH 48920 ♂—Zaire: Medje
    AMNH 48923 ♀—same as ♂
25. *Tadarida (Mops) brachyptera* (TM BRACH, TMb)
    AMNH 233868 ♀—Uganda: Buganda; Sese Is., Bugala
26. *Tadarida (Mops) condylura* (TM CONDA, TMcd)
    BJH 2462 ♂—Kenya: Kilifi Veterinary Station
    USNM 421490 ♀—Dahomey: Ketou, eastern region; 7° 21′ N, 2° 37′ E
27. *Tadarida (Mops) congica* (TM CONGA, TMcg)
    AMNH 241063 ♂—Cameroun: 25 km. NE Bertoua
    AMNH 48894 ♀—Zaire: Medje
28. *Tadarida (Mops) demonstrator* (TM DEMOA, TMd)
    AMNH 184432 ♂—Sudan: Bahr el Ghazal Prov.; Yirol Dist., Lake
        Nyibor
    AMNH 184428 ♀—same as ♂
29. *Tadarida (Mops) leonis* (TM LEONA, TMl)
    AMNH 241079 ♂—Cameroun: 30 km. E Nanga-Emboko
    USNM 414252 ♀—Ghana: Western region, 32 miles W Prestea;
        5° 23′ N, 2° 28′ W
30. *Tadarida (Mops) midas* (TM MIDAA, TMmi)
    AMNH 184388 ♂—Sudan: Bahr-el-Ghazal; Yirol Dist., Lake Nyibor
    BJH 3332 ♀—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
31. *Tadarida (Mops) mops* (TM MOPSA, TMmo)
    AMNH 234212 ♂—Malaya: Selangor; Fraser's Hill
    BM 19.8.20.2 ♀—Malaya: Selangor; Kuala Lampur
32. *Tadarida (Mops) nanula* (TM NANUA, TMna)
    AMNH 48863 ♂—Zaire: Niangara
    BJH 3327 ♀—Kenya: West Pokot Dist.; 2 miles S Sigor, Wei-Wei River
33. *Tadarida (Mops) niangarae* (TM NIANG, TMng)
    AMNH 48901 ♂ type—Zaire: Niangara
34. *Tadarida (Mops) niveiventer* (TM NIVEI, TMni)
    AMNH 85525 ♂—Angola: Chitau
35. *Tadarida (Mops) sarasinorum sarasinorum* (TM SARSA, TMs)
    AMNH 109078 ♂—Celebes: Peleng Is.
    AMNH 109063 ♀—same as ♂
    Tadarida (Mops) sarasinorum lanei
        *AMNH 241951 ♂—Philippine Is.: Mindanao; Cotabato, Saub
        *AMNH 241990 ♀—same as ♂

36. *Tadarida (Mops) trevori* (TM TREVO, TMtr) ˛
        AMNH 49250 ♀ type—Zaire: Faradje
37. *Tadarida (Mops) thersites* (TM THERA, TMth)
        USNM 25208 ♂—Equatorial Guinea: Moka
        USNM 25210 ♀—same as ♂
38. *Xiphonycteris spurrelli* (XIPHONYC, X)
        USNM 395721 ♂—Equatorial Guinea: Moka
39. *Tadarida (Mormopterus) acetabulosus* (TR ACETA, TRa)
        BM 99.11.27.1 ♂—Mauritius
        BM 6.11.1.9 ♀—Southern Ethiopia
40. *Tadarida (Mormopterus) beccarii* (TR BECCR, TRb)
        AMNH 159401 ♂—Papua: Fergusson Is.; Mapamoiwa
41. *Tadarida (Mormopterus) jugularis* (TR JUGUA, TRj)
        USNM 328773 ♂—Madagascar: Tulear Prov.; Tsihombe
        USNM 328774 ♀—same as ♂
42. *Tadarida (Mormopterus) kalinowskii* (TR KALIN, TRk)
        AMNH 165625 ♂—Peru: Libertad; Trujillo
43. *Tadarida (Mormopterus) loriae* (TR LORIA, TRl)
        AMNH 194196 ♂—Australia: N Queensland; Cape York, China Camp
        AMNH 154744 ♀—Australia: N Queensland; Cape York, Helenvale, 20
            miles S Cooktown
44. *Tadarida (Mormopterus) minutus* (TR MINUA, TRm)
        AMNH 4195 ♂ type—Cuba: Trinidad
        AMNH 4914 ♀—same as ♂
45. *Tadarida (Mormopterus) norfolkensis* (TR NORFA, TRn)
        AMNH 154735 ♂—Australia: Cape York; Mossman
        AMNH 154737 ♀—Australia: Cape York; Cairns
46. *Tadarida (Mormopterus) phrudus* (TR PHRUD, TRph)
        AMNH 91553 ♂—Peru: Machu Picchu
47. *Tadarida (Mormopterus) planiceps* (TR PLANA, TRpl)
        AMNH 220093 ♂—Australia: Victoria; Carisbrook
        AMNH 220094 ♀—Australia: Victoria; 18 miles NW Underbool
48. *Cheiromeles parvidens* (C PARVID, Cp)
        AMNH 241942 ♂—Philippine Is.: Mindanao; Cotabato, Saub
49. *Cheiromeles torquatus* (C TORQUT, Ct)
        ROM 44147[2] ♀—Philippine Is.: Negros Is.
        *AMNH 103922 ♀—Borneo (NE): Peleben
50. *Cynomops brachymeles* (CP BRACA, CPb)
        AMNH 239235 ♂—Paraguay: Guaira; Villarrica
        AMNH 23800 ♀—Paraguay: Sopucay
51. *Cynomops greenhalli* (CP GREEA, CPg)
        AMNH 183868 ♂—Panama: Canal Zone; Cocoli
        AMNH 176285 ♀—Trinidad: Port of Spain; Botanic Gardens
52. *Cynomops planirostris* (CP PLANA, CPp)
        AMNH 234457 ♂—Paraguay: Dept. Olimpo; Fuerte Olimpo
        AMNH 17096 ♀—Venezuela: Maripa

---

[2]It came to my attention only after my study was completed that this specimen may not
be true *torquatus*.

53. *Eumops auripendulus* (E AURIPA, Ea)
>   AMNH 93851 ♂—Brazil: Rio Amazon, N bank; Faro
>   AMNH 93855 ♀—same as ♂
54. *Eumops bonariensis* (E BONARA, Eb)
>   AMNH 205653 ♂—Uruguay: Dept. Rio Negro; Arroyo Negro, 15 km S
>   Paysandu
>   AMNH 205661 ♀—same as ♂
55. *Eumops glaucinus* (E GLAUCA, Eg)
>   AMNH 207926 ♂—Colombia: Dept. Cundinamarca; Bogota
>   AMNH 130700 ♀—Venezuela: Rio Tocuyo
56. *Eumops hansae* (E HANSAA, Eh)
>   LSU 11487 ♂—Costa Rica: Puntarenas; 10 miles S Palmar Sur
>   USNM 310278 ♀—Panama: Darien; Tacarcuna
57. *Eumops maurus* (E MAURUS, Em)
>   BM 1.6.4.34 ♂ type—Guiana: Kanuku Mts.
58. *Eumops perotis perotis* (E PEROTA, Ep)
>   MSB 4300 ♂—Arizona: Pima Co.; Tucson
>   MSB 31266 ♀—New Mexico: Hidalgo Co.; 32 miles S Rodeo
>   *AMNH 185208 ♂—Argentina: Yuto; Jujuy
>   *Eumops perotis trumbulli*
>   *AMNH 97016 ♂—Brazil: R. Tocantins; Mocajuba
>   *AMNH 97022 ♀—same as ♂
59. *Eumops underwoodi* (E UNDERA, Eu)
>   UA 8112 ♂—Arizona: Pima Co.; ca. 10 miles NNW Sasabe, Encinas
>   Wash, Baboquivari Mt., T21S, R7E
>   MSB 10697 ♀—Arizona: Pima Co.; Garcia Represso, 2 miles E Sasabe
60. *Molossops temminckii* (MP TEMMA, MP)
>   AMNH 186950 ♂—Argentina: Yuto; Jujuy
>   AMNH 181537 ♀—same as ♂
61. *Molossus ater* (M ATERA, Ma)
>   AMNH 183317 ♂—Colombia: Norte de Santander; Cucuta
>   MSB 31532 ♀—Mexico: Sinaloa; Rio Magistral, 8.4 miles E Concordia
>   on Hwy. 40
62. *Molossus bondae* (M BONDAA, Mb)
>   AMNH 212908 ♂—Panama: Canal Zone; Ft. Sherman, 5 km. W Colon
>   AMNH 183322 ♀—Colombia: Norte de Santander; Cucuta
63. *Molossus coibensis* (M COIBEA, Mc)
>   MSB 27876 ♂—Panama: Canal Zone; Barro Colorado Is.
>   MSB 29170 ♀—same as ♂
64. *Molossus molossus molossus* (M MOLOSS, Mm)
>   AMNH 212295 ♂—Colombia: Dept. Cundinamarca; Sasaima
>   *Molossus molossus barnesi*
>   *BM 5.1.8.7 ♀ type—French Guiana: Cayenne
>   *Molossus molossus lambi*
>   *AMNH 217440 ♂—Guatemala: Dept. Jutiapa; Col Montufar, ca. 12
>   miles S Pedro Alvarado
>   *Molossus molossus pygmaeus*
>   *AMNH 30393 ♂ topotype—Netherlands West Indies: Curacao

65. *Molossus pretiosus* (M PRETIA, Mp)
    AMNH 23780 ♂—Venezuela: La Guaira
    AMNH 23781 ♀—same as ♂
66. *Molossus sinaloae* (M SINALA, Ms)
    AMNH 204985 ♂—Yucatan: Cenote, 2 km. N Hunucma
    AMNH 41190 ♀—Nicaragua: Sioux Plantation, 125 miles up Rio Grande, Sixicuas Creek
67. *Molossus trinitatus* (M TRINIA, Mt)
    AMNH 179987 ♂ type—Trinidad: Port of Spain; Belmont
    AMNH 7521 ?—Trinidad: Port of Spain
68. *Myopterus albatus* (MYOP ALB, MYa)
    AMNH 48855 ♀—Zaire: Niangara
69. *Myopterus whitleyi* (MYOP WHA, MYw)
    BM 26.7.6.99 ♂—Zaire: Kasai; Luluabourg
    BM 26.11.1.46 ♀—Zaire: Kasai; Luluabourg
70. *Neoplatymops mattogrossensis* (NEOPLATA, N)
    AMNH 149150 ♂—Venezuela: Amazonas Terr.; Tapara, upper Rio Cunucunuma NW Cerro Dvida
    ROM 32984 ♀—Guiana: Rupununi Dist.; 15 miles E Dadanawa
    *ROM 32986 ♂—same as ROM ♀
71. *Otomops martiensseni* (OTO MARA, Om)
    AMNH 88115 ♂—Angola: Chitau
    BJH 2337 ♀—Kenya: Rift Valley; cave on Mt. Suswa, 35 miles WNW Nairobi
72. *Otomops papuensis* (OTO PAPU, Op)
    BM 73.136 ♂—New Guinea: Mt. Suckling; Maul
73. *Otomops secundus* (OTO SECA, Os)
    BM 50.982 ♂ type—New Guinea (NE): Upper Ramu River Plateau, Tapu
    BM 50.979 ♀—same as ♂
74. *Otomops wroughtoni* (OTO WROA, Ow)
    BM 13.4.9.3 ♂—India: Talawadi; Parapede Cave
    BM 13.4.9.6 ♀—same as ♂
75. *Platymops setiger* (PLATYMOA, P)
    BJH 2473 ♂—Kenya: 10 miles N Kiboko, ca. 100 miles SE Nairobi
    AMNH 219867 ♀—Kenya: Rift Valley; Lake Baringo, Kampi ya Samaki
76. *Promops centralis* (PRO CENA, PRc)
    AMNH 126828 ♂—Honduras: La Paz; Los Encuentros
    AMNH 126854 ♀—Honduras: La Paz; El Pedrero
77. *Promops nasutus ancilla* (PRO NASU, PRn)
    AMNH 184647 ♀—Argentina: Jujuy; Yuto
    Promops davisoni
    *AMNH 34382 ?—Ecuador: Manavi, Rio de Oro
    *LSU 16639 ♀—Peru: Dept. Lima; Canete
78. *Sauromys petrophilus* (SAUROMYS, S)
    AMNH 165942 ♂—Botswana: Molepolole
79. Vespertilionidae—*Nyctalus nocula* (NYCTALUS, NY)
    AMNH 162809 ♂—Germany: Bavaria; Haag a/Amper

80. Vespertilionidae—*Mimetillus moloneyi* (MIMETILL, MI)
　　　USNM 424872 ♂—Ghana: Volta Region; Leblebi Agbesia, 6° 56′ N,
　　　0° 25′ E

Characters Used

I employed the exemplar method of Sneath & Sokal (1973, p. 183). Characters in my study included 56 morphometric measurements, 12 qualitative multistate codes, and eight ratios. The morphometric measurements are standard ones from the skull, wings, and body. Codes are features which are hard to measure, but which have been emphasized historically as being important in defining molossid species. Ratios used are those which have been used by other authors, or those which are proportional to a reliable size measurement. It could be argued that characters should be as uncorrelated as possible, but had only uncorrelated characters been used, many fewer measurements would have been taken, and some functionally important trends could have been missed. In addition, I think that maintaining a large number of characters gave rise to a robust arrangement of OTU's in the principal components analysis, so that changes in the number of OTU's or kinds of characters or both had little effect on the representation of the basic morphological relationship among the bats.

A preliminary study of 22 species indicated several characters that could be interpreted ecologically. I derived the final list of characters by removing the ones which could not be accurately measured or quantified and by adding ones which were related to functionally relevant morphological trends indicated by the study of 22 bats. For example, several characters concerned with the jaw were added which would better describe changes in that structure.

The qualitative multistate characters (codes) were the most difficult to handle because quantification involved substantial subjectivity. An overview of the variation among all the bats was attained before reasonable coding could be done. Here, the codes show degrees of change (qualitative multistates) and are made as continuous as possible. I did not include lower incisor number as a character.

Measurements were taken under a dissecting microscope and were carried to the nearest 0.1 mm with Helios dial calipers. For two measurements, width of angular process and height of condyle above the lower toothrow, a cross hair reticle in the microscope was necessary. For many of the dentary measurements, it was more convenient to use articulated mandibles rather than disarticulated ones. The scale in the drawings of the skulls is equal to 1 mm, and all drawings in Figures 9-20 are drawn to scale.

All 76 characters are described in detail below and are illustrated in Figure 1. Abbreviations used in the figures, tables, and text are given for each character.

General body characters

1. Head and body (HB)—length from tag or alcoholic specimen
2. Tail (TAIL)—length from tag or alcoholic specimen
3. Ear (EAR)—length from tag or alcoholic specimen
4. Hindfoot (HF)—length from heel to end of longest toenail on dry or wet specimen
5. Tibia (TIBIA)—length from knee joint at indentation between femur and tibia to distal end of tibia (not including tarsals)

6. Forearm (FA)—length from olecranon process to shallow notch proximal to thumb (including carpals)
7. Third metacarpal (3 META)—length from distal endpoint for FA to distal end of bone
8. Third metacarpal first phalanx (3M 1PHAL)—greatest length of bone
9. Third metacarpal second phalanx (3M 2PHAL)—greatest length of bone
10. Third metacarpal third phalanx and tip (3M TIP)—length from proximal end of third phalanx to distal end of cartilaginous tip (curve of tip measured in two straight lines breaking at greatest point in curve)
11. Fourth metacarpal (4 META)—length from distal endpoint for FA to distal process of bone
12. Fourth metacarpal first phalanx (4M 1PHAL)—greatest length of bone
13. Fourth metacarpal second phalanx (4M 2PHAL)—greatest length of bone (no cartilage included)
14. Fifth metacarpal (5 META)—length from distal endpoint for FA to distal process of bone
15. Fifth metacarpal first phalanx (5M 1PHAL)—greatest length of bone
16. Fifth metacarpal second phalanx (5M 2PHAL)—greatest length of bone plus cartilaginous tip
17. Digit three (DIGIT 3)—sum of metacarpal 3, phalanges, and tip
18. Digit four (DIGIT 4)—sum of metacarpal 4 and phalanges
19. Digit five (DIGIT 5)—sum of metacarpal 5, phalanges, and tip
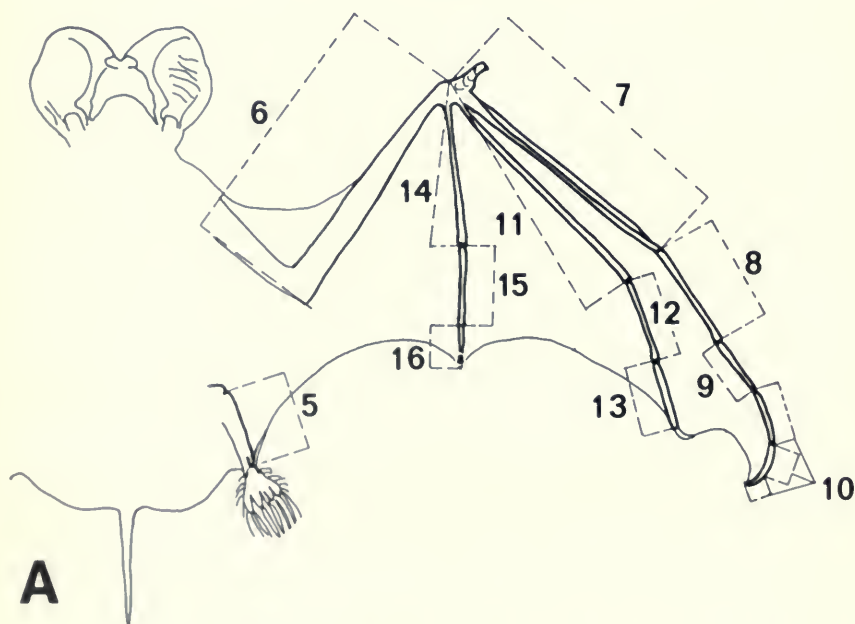
FIG. 1. The limits of each measurement on the wing and body (A) and skull and mandible (B). Numbers correspond with the measurements described in Materials and Methods.

FIGURE 1.

13
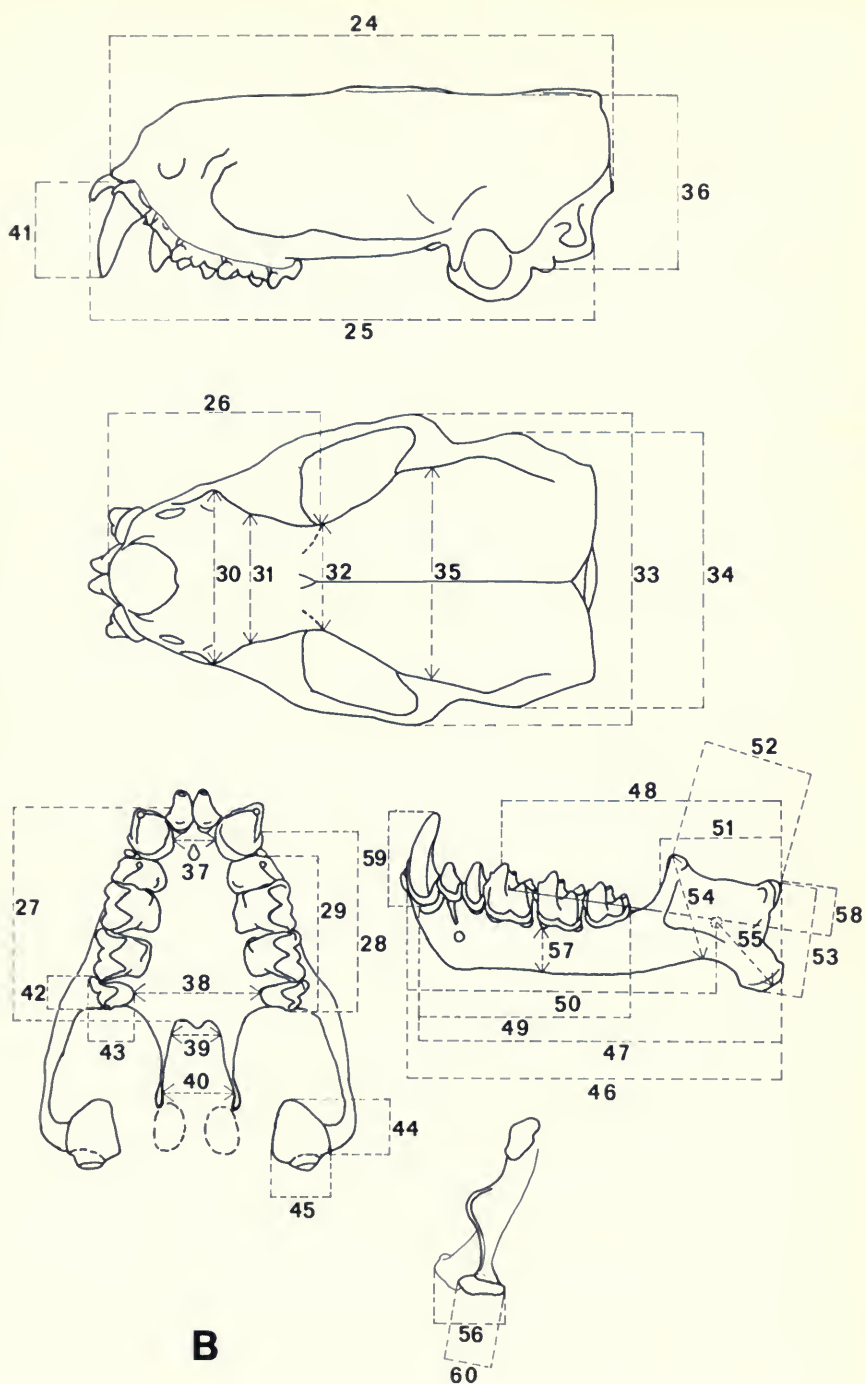
R20. Aspect ratio (ASPECT)—DIGIT 3 plus FA divided by DIGIT 5

R21. Tip index (TIP INDX)—DIGIT 3 divided by DIGIT 3 plus FA, times 100

R22. Digit three divided by digit five (D3 I D5)

R23. Ear divided by forearm (EAR I FA)

Skull measurements

24. Greatest skull length (GSL)—from posteriormost part of occipital to anteriormost point of the premaxillary bone (taken on a line parallel to line connecting foramen magnum and anterior point on the premaxillary)

25. Condyloincisive length (CON INCI)—from occipital condyle to anteriormost point of upper incisors

26. Rostral length (ROST LEN)—from cribiform plate to anteriormost point of premaxillary bone

27. Palatal length (PALATE)—from posterior border of hard palate to anterior border of premaxillary bone

28. Maxillary toothrow (MTR)—length from anterior alveolar border of canine to posterior alveolar border of M^3

29. Upper molariform row (UP MOL R)—length from PM^4 to M^3 (alveolar)

30. Lacrimal width (LACR WID)—width across rostrum dorsally at protuberances near lacrimal canals

31. Interorbital width (INTORB W)—width across rostrum dorsally between lacrimals and least constriction

32. Postorbital width (POST ORB)—dorsal width at most constricted part of skull

33. Zygomatic breadth (ZYGO BR)—width taken across zygomatic arches at widest point near posterior junction with braincase

34. Breadth at mastoids (MASTOID)—greatest breadth at mastoid processes

35. Breadth braincase (BR BCASE)—breadth just dorsal to posterior juncture of zygomatic process

36. Height of braincase (BCASE HT)—from basisphenoid and basioccipital bones to top of braincase on either side of sagittal crest

37. Width at upper canines (C1 C1)—width between alveolar borders of upper canines

38. Width at upper molars (M3 M3)—width between alveolar borders of upper third molars

39. Width at anterior pterygoids (ANT PTER)—width at anterior divergence of pterygoid processes

40. Width at posterior pterygoids (POSTPTER)—width at posterior part at middle depth of pterygoid processes

41. Height upper canine (UP CANIN)—greatest length from point immediately dorsal to cingulum to end of tooth (not taken if too worn)

42. Length M^3 (M3 LENG)—anterior-posterior length of tooth

43. Width M^3 (M3 WIDTH)—greatest lateral-medial width of tooth

44. Length glenoid fossa (GLENO L)—anterior-posterior length of fossa from middle of face of postglenoid process to anteriormost rim of fossa

45. Width glenoid fossa (GLENO W)—greatest lateral-medial width of fossa (light must be good to see fossa rims)

Dentary characters

46. Dentary length (DENT LEN)—from midpoint of mandibular condyle to anteriormost point of dentary
47. Condylocanine length (CON CANI)—from midpoint of condyle to anterior border of alveolus of lower canine
48. Condyle to M_1 (COND M1)—length from midpoint of condyle to anterior face of protoconid on first lower molar
49. Lower toothrow (LOWER TR)—length from posterior alveolar border of M_3 to anterior alveolar border of C_1
50. Length mandibular foramen to anterior dentary (FOR ANT)—from medial foramen at base of coronoid process to anteriormost point of dentary
51. Condylo-coronoid length (CON CORO)—from middle of longitudinal axis of condyle to anterior face of coronoid directly opposite
52. Moment arm of temporal (MOM1 COR)—length from middle of condyle to tip of coronoid process
53. Moment arm of masseter (MOM2 ANG)—length from middle of condyle to tip of angular process
54. Height of coronoid (CORO HT)—from indentation of ventral mandibular border to tip of coronoid (easiest to take on articulated mandibles)
55. Length angular process (ANGUL L)—from mandibular foramen to tip of angular
56. Width angular process (ANGUL W)—actually the amount of splaying laterally of the angular. Taken with vertical cross hair of microscope lined up with medial border of condyle and horizontal cross hair at the posterior tips of both angular processes. Calipers are braced on a finger to line up one side with the vertical.
57. Dentary thickness (DENTTHIC)—width of dentary at base of protoconid of M_2 taken on the lateral surface (calipers must be braced)
58. Height of condyle above the toothrow (TR CON H)—horizontal cross hair in microscope aligned with valleys at the bases of hypoconid and protoconid of M_1 and M_3 (these have less wear than the tops of the cusps). Height taken from this line to top of condyle with braced calipers.
59. Height lower canine (LO CANIN)—greatest length from point immediately ventral to cingulum to top of tooth (not taken if too worn)
60. Length condyle (CONDY L)—medial-lateral length of mandibular condyle
R61. Condyle height/dentary length (CONHT DL)—TR CON H divided by DL
R62. Dentary thickness/dentary length (DTHIC DL)—DENTTHIC divided by DL
R63. Moment arm index (M1+M2 DL)—MOM1 COR (temporal) plus MOM2 ANG (masseter) divided by DL
R64. Coronid height/dentary length (COR H DL)—CORO HT divided by DL

Qualitative multistate characters (codes)

C65. Incisive foramina (INCI FOR)—degree of emargination of anterior palate, states as follow from closed to open:
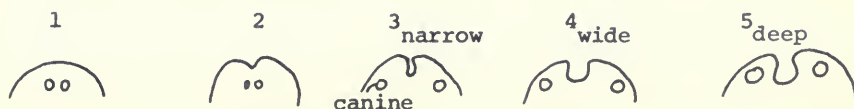
C66. Shape of cusp on M^3 (N SHAPE)—degree of change of cusp pattern on upper third molar, states as follow from N to V shape:

| 1 | 2 | 3 | 4 | 5 | 6 |

posterior arm
equal to or longer
than anterior arm
      over ½   less ½
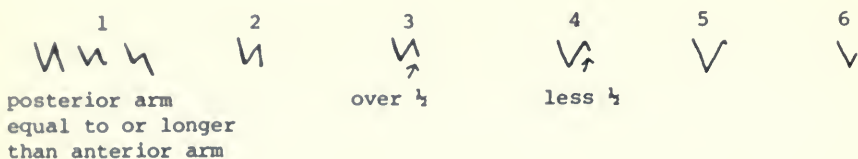
C67. Development of PM^3 (PREMOLAR)—degree of development of upper third premolar, states as follow, from absence to presence:

1	2	3	4
none	small (or vestigial)	moderate	large

C68. Development of metaconule on M^1 (M1 META)—states as follow, from slightly distinct to very distinct:

1	2	3
slight	moderate	very distinct

C69. Development of basisphenoid pits (BASI PIT)—states as follow, from none to very deep:

1	2	3	4	5
none	shallow	moderate	deep	very deep

C70. Development of anterior sagittal crest (A SAGITT)—states as follow, from slight to great:

1	2	3
none or slight	moderate	great

C71. Development of posterior sagittal crest (P SAGITT)—states as follow, from slight to great:

1	2	3
none or slight	moderate	great

C72. Development of lateral lambdoidal crest (L LAMBDO)—states as follow, from slight to great:

1	2	3
none or slight	moderate	great

C73. Development of superior lambdoidal crest (S LAMBDO)—states as follow, from slight to great:

1	2	3
none or slight	moderate	great

C74. Quality of ear junction (EAR JUNC)—states as follow, from well separated to well joined above the nose

1	2	3
well separated	V-shaped valley, not joined or only just joining at bases	well joined over nose with band

C75. Quantity of spoon hairs or spines on lips (HAIRYNES)—states as follow, from none to many:

1	2	3
none	few	many

C76. Degree of wrinkling on the upper lip (WRINKLES)—states as follow, from none to finely wrinkled:

1	2	3	4
none	few (less than 7)	many (more than 7)	many fine microscopic wrinkles (lips are skirt-like)

Statistical Analyses

The analyses used are from the packaged Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) developed by Rohlf et al. (1974). Data were standardized and analyzed by the following: principal components analysis or principal coordinates analysis (PCA), correlation, distance and reduced distance (Gower transformation), and phenograms by the unweighted pair-group method using arithmetic averages (UPMGA). All computer work was done on an IBM 360 model computer housed at the University of New Mexico Computer Center. A summary program, developed by G. Michael Schum at the University of New Mexico, producing all coefficients of variation, maximum and minimum distances of each OTU, and highest and least correlations of each OTU, was also employed. Good explanations of all the multivariate analyses used in this study can be found in Sneath & Sokal (1973).

Several major variations of the data were run and are listed as follows:

22 OTU's and 60 characters as a preliminary study
36 OTU's and 78 characters (raw measurements expressed as ratios)
155 OTU's and 65 characters (raw + codes) as a grouping study
80 OTU's and 53 characters (raw)
80 OTU's and 65 characters (raw + codes)
80 OTU's and 64 characters (raw + ratios)
80 OTU's and 76 characters (raw + codes + ratios)

All descriptions are based on the analysis with 80 OTU's, including 78 molossid species and two vespertilionid species; and 76 characters including 56 raw measurements, eight ratios, and 12 codes. The principal components analysis (PCA) proved to be a robust technique, because changing the number of OTU's or type of characters or both had little effect on the representation of the basic pattern of OTU's on the first few principal components.

I used several techniques for analysis because one alone does not adequately represent the multivariate data. The principal components analysis is an ordination technique and reveals clusters of phenetically similar bats. The distance

and correlation analyses are clustering techniques and detect nearest neighbor relationships.

In my principal components analysis, component I is a size component as it is in many biological studies where many size-related morphological features were measured. This first component accounts for 60 per cent of the total variation in the data. The second, third, and fourth components account for 12, 6, and 3 per cent of the variation, respectively. These components are shape-related. Because size does account for so much of the variation in the data and thus may obscure other trends, I think it is desirable to look only at the shape-related components to see how phenetically similar the bats are, whether large or small. I think shape-related morphology is more important in determining the phenetic and evolutionary relationships among the bats, whereas the size-related morphology is more important in determining the ecological relationships among the bats. Consequently, the first component can be eliminated when necessary, and only the second, third, and fourth components studied. This procedure, called "size-out," essentially subtracts the contribution of the first component from the distances among the OTU's (see Sneath & Sokal, 1973, pp. 172–173, for details). The size-out PCA is very similar to an earlier PCA done on all ratio data. I use size-out extensively for the morphological descriptions of the groups and in the examination of the evolutionary relationships. I use combined size and shape components (size-in) to support the morphological description, but primarily to analyze faunal composition.

Other Methods

The analysis of fecal samples that I used is one modified after Black (1974). I stained the fecal material with eosine, let it dry, put a portion on a slide, and weighed the exact amount with an analytical balance. I covered the weighed portion with Per-Mount and coverslip and let it dry. I took three different counts of moth scales in a 10- by 10-mm grid in a Wild M5 dissecting microscope and made an average for the sample. The result was an estimated count of scales per gram of fecal material.

GENERAL DESCRIPTION OF THE PRINCIPAL COMPONENTS

Because the first component is highly correlated with size, nearly all of the raw measurements are highly positively correlated with this axis. The largest bats are on the far positive end, and the smallest, on the negative end (fig. 2). As an example of the sizes involved, *Cheiromeles parvidens* has a GSL[3] of 30 mm, whereas *Tadarida (Mormopterus) minutus* has a GSL of 13 mm (table 1, appendix A). A frequency distribution of GSL's shows this measurement to be distributed log normally and to correspond well with the frequency distribution of OTU's on the first principal component (fig. 3).

Highly correlated with the second principal component are characters related to the shape of the jaw and teeth. The highest character loadings on all components are listed in Table 2. The second component or axis can be viewed in

[3]The GSL is used as a measure of size in the molossids because weights, probably the best measure, were not always available. Forearm length does not always correspond to general body size (Verschuren, 1957), and head and body length from the tag is undependable.

TABLE 1. Greatest skull lengths of molossid bats ordered from smallest to largest (*Sauromys* and *Platymops* are listed under *Mormopterus; Molossops, Neoplatymops, Cynomops, Myopterus,* and *Cheiromeles,* under Conglomerate; and *Promops,* under *Otomops*).

Size (mm.)	Tadarida	Chaerephon	Mops	Mormopterus	Conglomerate	Eumops	Molossus	Otomops
13.0–13.9				TR MINUA	MP TEMMA NEOPLATA			
14.0			XIPHONYC	TR ACETA TR LORIA				
15.0			TM NANUA	TR NORFA TR KALIN TR PLANA TR PHRUD PLATYMOP	CP PLANA		M COIBEA	
16.0	T BRASIA	TC CHAPI		TR JUGUA				
17.0		TC MAJOR TC PUMIA TC BEMMI	TM LEONA	SAUROMYS	CP GREEA MYOP WHA		M MOLOSS M BONDAA	PRO NASU
18.0	T LATICA T ANSORA	TC RUSSA TC NIGEA	TM BRACH TM THERA	TR BECCR			M TRINIT	
19.0	T FEMORA T AEGYPA	TC JOHOR TC PLICA TC BIVIA	TM SARSA			E HANSAA E BONARA	M GINALA :	OTO PAPU
20.0	T AURISA		TM DEMOA TM CONDA		CP BRACA	E MAURUS	M PRETIA	PRO CENA
21.0	T KUBORI	TC ALOYA TC JOBEN	TM NIVEI TM MOPSA				M ATERA	OTO SECA
22.0	T FULMIN T LOBATA							
23.0	T MACROA T AUSTRA		TM NIANG TM TREVO		MYOP ALB	E GLAUCA E AURIPA		
24.0	T TENIOA T AFRICA							OTO WROA
25.0			TM CONGA					
26.0								
27.0			TM MIDAA			E UNDERA		OTO MARA
28.0								
29.0					C TORQUT			
30.0					C PARVID	E PEROTA		

several plots: with component I in Figure 2A and with components III and IV in Figure 4. In all figures, the relative thickness of the dentary is greater in bats on the positive end as are three other characters related to the jaw: relative sum of muscle moment arms, relative height of coronoid process, and relative height of mandibular condyle above the toothrow. Bats on the positive end also have V-shaped (and shorter) M^3's and little or no development of PM^3. Development of sagittal and lambdoidal crests is greater in bats on the positive end, and the number of spoon hairs or spines around the mouth is higher in bats on the positive end, but they have shorter ears and no palatal emargination.

In contrast, bats on the negative end of axis II have the following morphological features: thin jaws, condyles in line with the toothrow, low coronoid processes, N-shaped (longer) M^3's, well-developed PM^3's, undeveloped cranial crests, a lesser degree of hairiness, longer ears, and a wide palatal emargination. Illustrative extremes on axis II are *Cheiromeles* and *Molossus* on the positive, thick-jawed end, and *Otomops* and *Tadarida macrotis* on the negative, thin-jawed end.

FIGURE 2.
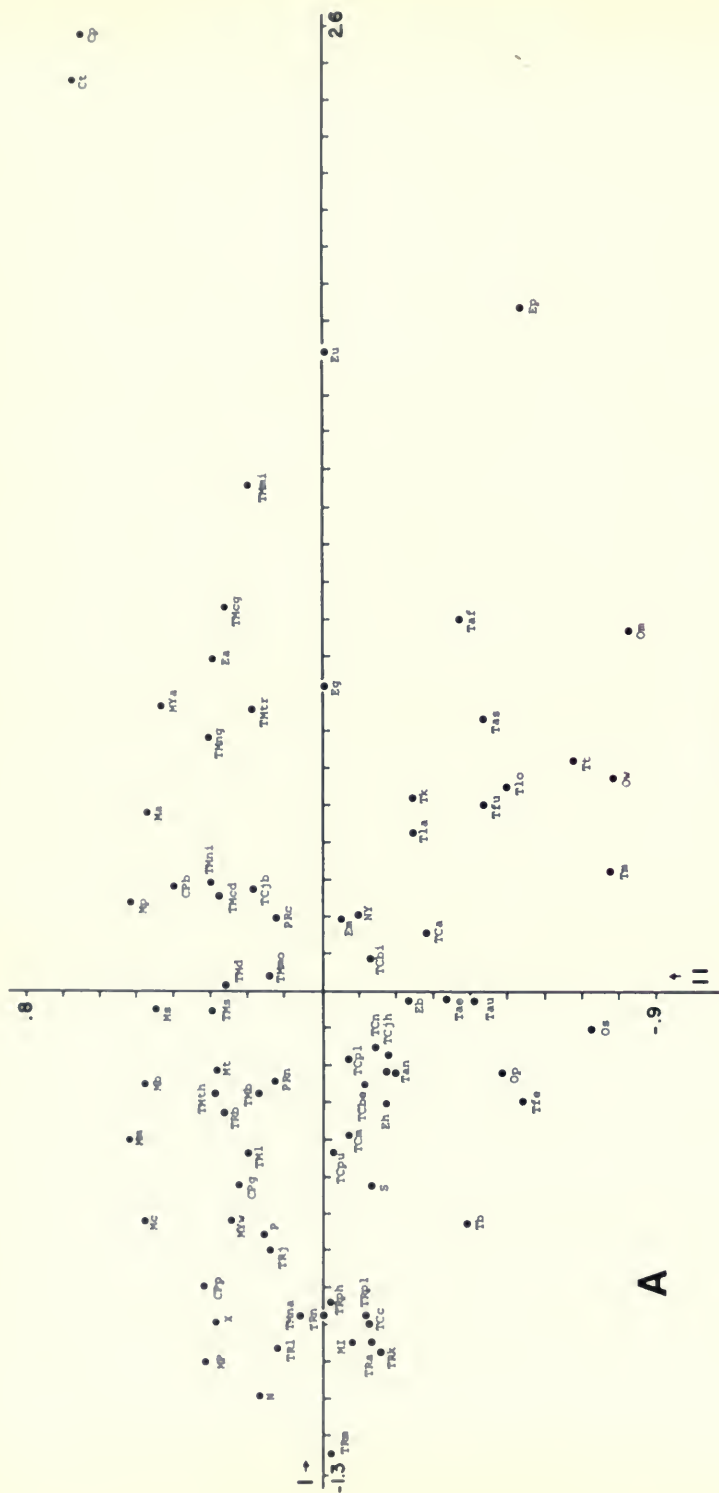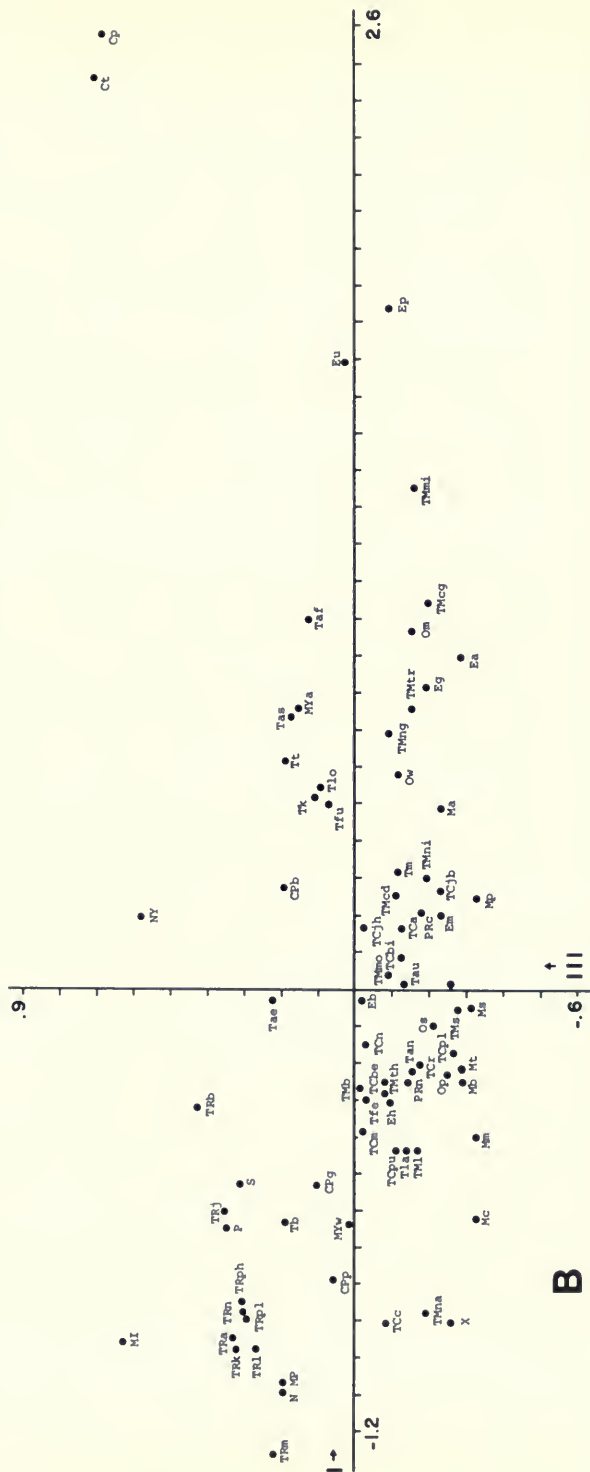
Fig. 2. Two-dimensional graphs of the size component (PC I) and components II and III. Abbreviations are listed in Materials and Methods. **A**, PC I versus PC II; **B**, PC I versus PC III.

21
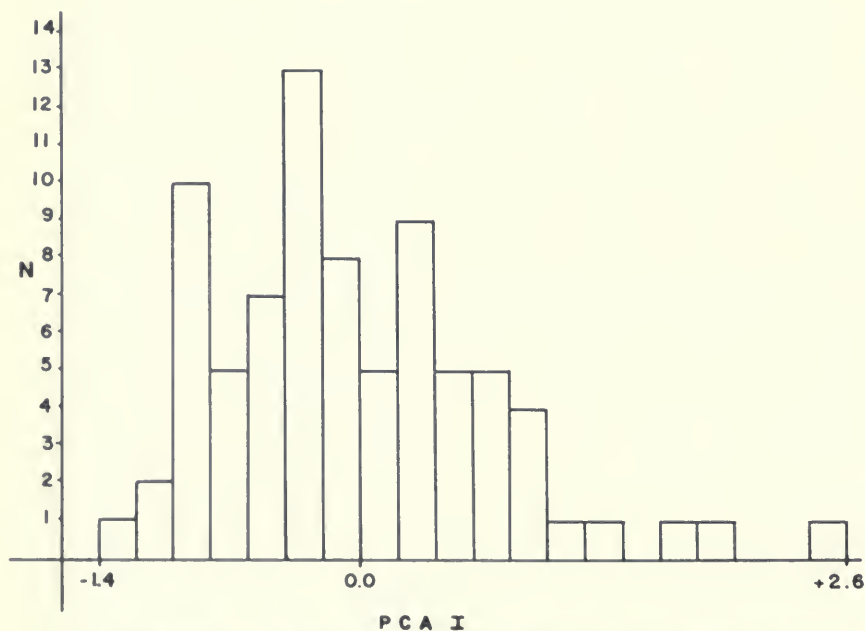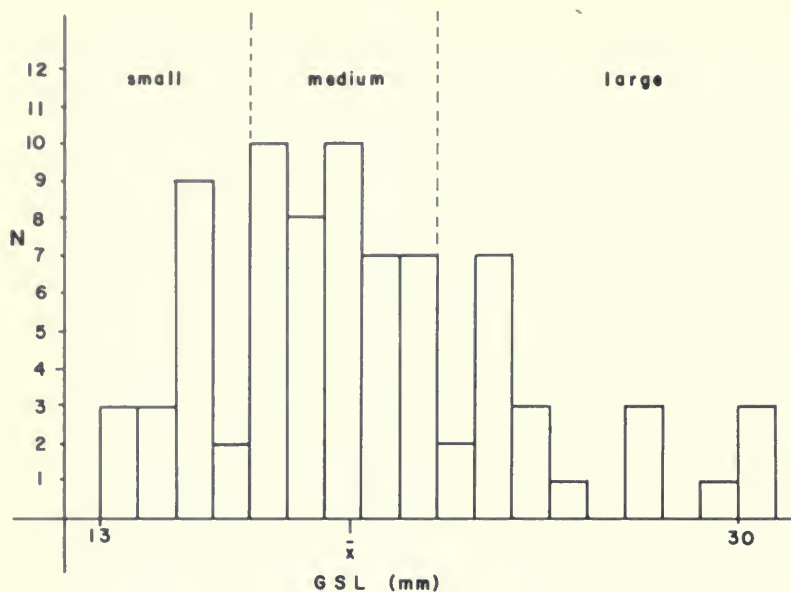
FIG. 3. Comparison of frequency distributions of the character, greatest skull length, and principal component I. The dashed lines delineate small, medium, and large bats and are drawn at approximately one-half standard deviation units from the mean.

TABLE 2. Twenty most highly correlated characters for each of the first four principal components and percentage of the total variation accounted for by each factor.

	Component I		Component II		Component III		Component IV	
Character	DENT LEN	.984	DTHIC DL	.855	EAR JUNC	-.701	L LAMBDO	.733
Correlations	CON CANI	.984	M1+M2 DL	.839	A SAGITT	-.688	4M 2PHAL	-.595
	COND M1	.981	COR H DL	.749	BASI PIT	-.552	EAR JUNC	-.467
	UP MOL R	.977	N SHAPE	.720	COR H DL	.543	EAR I FA	-.447
	GSL	.976	CONHT DL	.707	INTORB W	.488	PREMOLAR	-.400
	LOWER TR	.974	PREMOLAR	-.690	INCI FOR	.453	3M TIP	-.360
	ZYGO BR	.974	TR CON H	.646	N SHAPE	-.424	TAIL	.350
	HEAD BOD	.971	P SAGITT	.638	ANGUL W	-.412	C1 C1	-.325
	CON INCI	.970	S LAMBDO	.636	LACR WID	.409	S LAMBDO	-.322
	MTR	.964	HAIRYNES	.600	C1 C1	.394	INCI FOR	-.263
	DIGIT 3	.963	M3 LENG	-.588	CONHT DL	.391	CONHT DL	-.255
	DIGIT 4	.960	WRINKLES	-.553	TR CON H	.387	D3 I D5	-.250
	MOM1 COR	.959	EAR	-.549	CORO HT	.377	HAIRYNES	-.234
	BCASE BR	.955	EAR I FA	-.523	HAIRYNES	-.362	TR CON H	-.232
	3M 2PHAL	.953	INCI FOR	-.510	POST ORB	.349	5M 2PTIP	.227
	CON CORO	.952	DENYTHIC	.469	D3 I D5	-.327	ASPECT	-.224
	MASTOIDB	.950	CORO HT	.450	S LAMBDO	-.317	4M 1PHAL	.186
	3M 1PHAL	.943	M1 META	-.438	4M 2PHAL	.291	5 META	.172
	PALATE L	.941	TIP INDX	.435	M3 LENG	.281	P SAGITT	.169
	GLENO W	.941	ANGUL W	.393	P SAGITT	-.276	M3 WIDTH	.166
% variation	60.29		12.16		6.16		3.74	
Accumulated %	60.29		72.44		78.60		82.35	

23
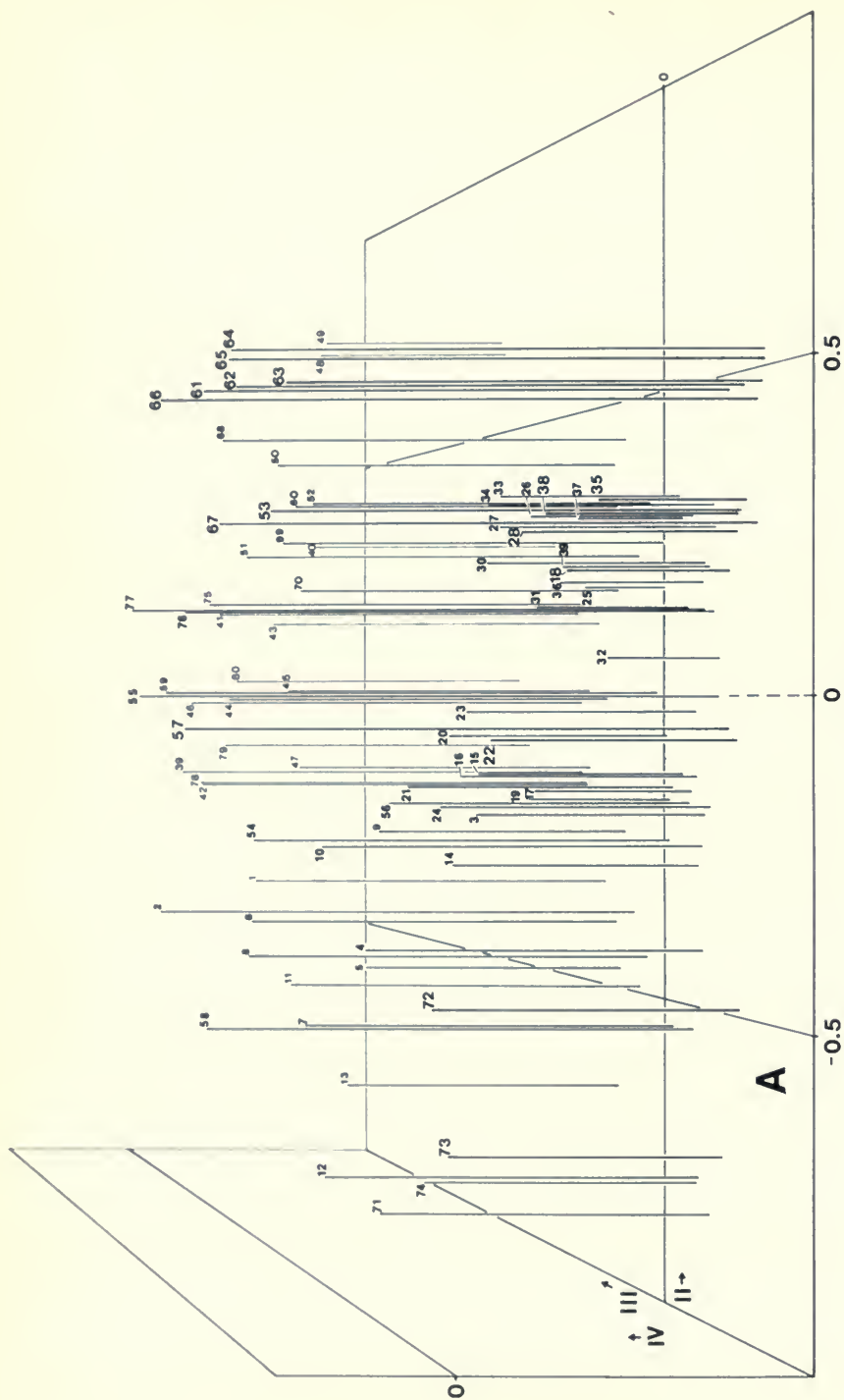
FIGURE 4.

Figure 4.
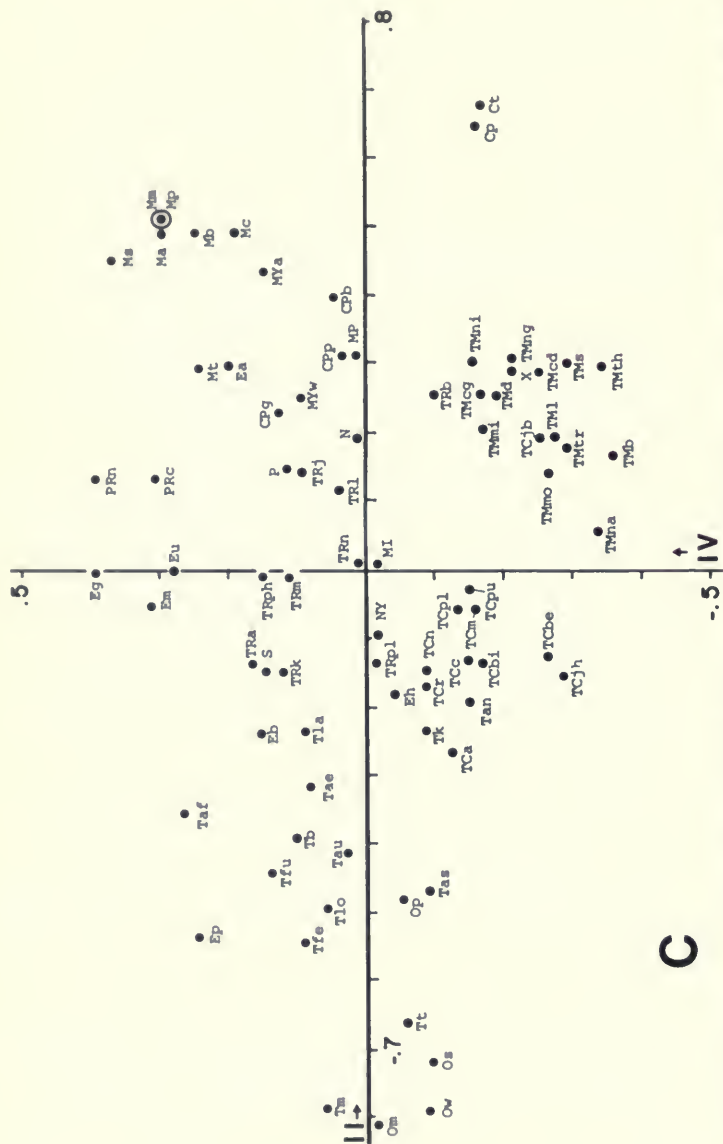
Fig. 4. Three- and two-dimensional graphs of the jaw component (PC II) and components III and IV. Abbreviations are listed in Materials and Methods. **A**, PC II versus PC IV; **B**, PC II versus PC III; and **C**, PC II versus PC IV.

26

Principal components III and IV are more obscure in their meaning than components I and II. There are fewer highly correlated characters in each, and each accounts for less of the total variation. In general, bats on the negative end of axis III (fig. 4A) have ears facing forward and joined above the nose, well-developed anterior sagittal crest, little development of the coronoid process, deep basisphenoid pits, and faces narrow at the interorbital width. Bats on the positive end generally have widely separated, laterally facing ears, well-developed coronoid processes, shallow basisphenoid pits, and wide faces.

On the fourth component, bats with a well-developed lateral lambdoidal crest and short second phalanx of digit IV are on the positive end, and bats with an undeveloped crest and long phalanx are on the negative end (fig. 4B). If the bats are not extreme in both characters, they are not represented well on this component.

FUNCTIONAL MORPHOLOGY

The jaw structure in molossids is variable: New World extremes are *Molossus ater* on one end, with a short, stout mandible and well-developed sagittal crest; and *Tadarida macrotis* on the other, with a long, delicate mandible and an undeveloped sagittal crest. Likewise, molossids in the Old World have a similar pattern of variation: *Cheiromeles* on the same end with *Molossus ater*; and *Otomops*, with *Tadarida macrotis* (figs. 4, 5). Evidence that I present with each molossid group indicates that the short, thick-jawed bats are eating hard-shelled foods, and the long, delicate-jawed ones are eating soft-shelled items.

Bone thickens at points where more stress occurs (Hildebrand, 1974, pp. 431–456). Maynard Smith & Savage (1959) pointed out that carnivores which take struggling prey have thickened dentaries. Along with this dentary thickening, carnivores also have an increase in the bulk and area of origin of the *m. temporalis*. Some molossid bats, such as *Molossus*, show the same attributes, namely an increased dentary thickness and a well-developed sagittal crest. Molossids of this type also have a greater area of insertion for *m. temporalis* at the coronoid process and possibly an increased area for insertion of the masseter (or leverage) onto the more laterally flaring angular process. Both jaw muscles in *Molossus ater* are developed to a tremendous extent compared with those in *Tadarida macrotis* (fig. 6). The temporal muscle of the first bat nearly encases the braincase from the eye socket to the lambdoidal crest, and the masseter forms a fat, fistlike muscle at the cheek. *Tadarida macrotis*, on the other hand, has no such development of those muscles. The Old World extremes, *Cheiromeles* and *Otomops*, have similar differences in muscle development.

Another characteristic on the second principal component which seems important functionally but is more difficult to explain is the relative height of the mandibular condyle above the lower toothrow. Though this trait is correlated with increasing dentary thickness ($r = .502$), it seems to be greatest in the small bats. Regression analyses in Figure 7 better illustrate these traits as especially characteristic of the small *Mormopterus* and *Mormopterus*-like bats. In carnivores, the condyle is in line with the toothrow, whereas in herbivores, the condyle is well above the toothrow (Maynard Smith & Savage, 1959; Crompton & Heiimäe, 1969). Supposedly, in herbivores, the elevated condyle gives a more uniform bite force along the toothrow (Crompton & Heiimäe, 1969). Storch (1968) and Kallen & Gans (1972) mentioned that the angle of approach of lower
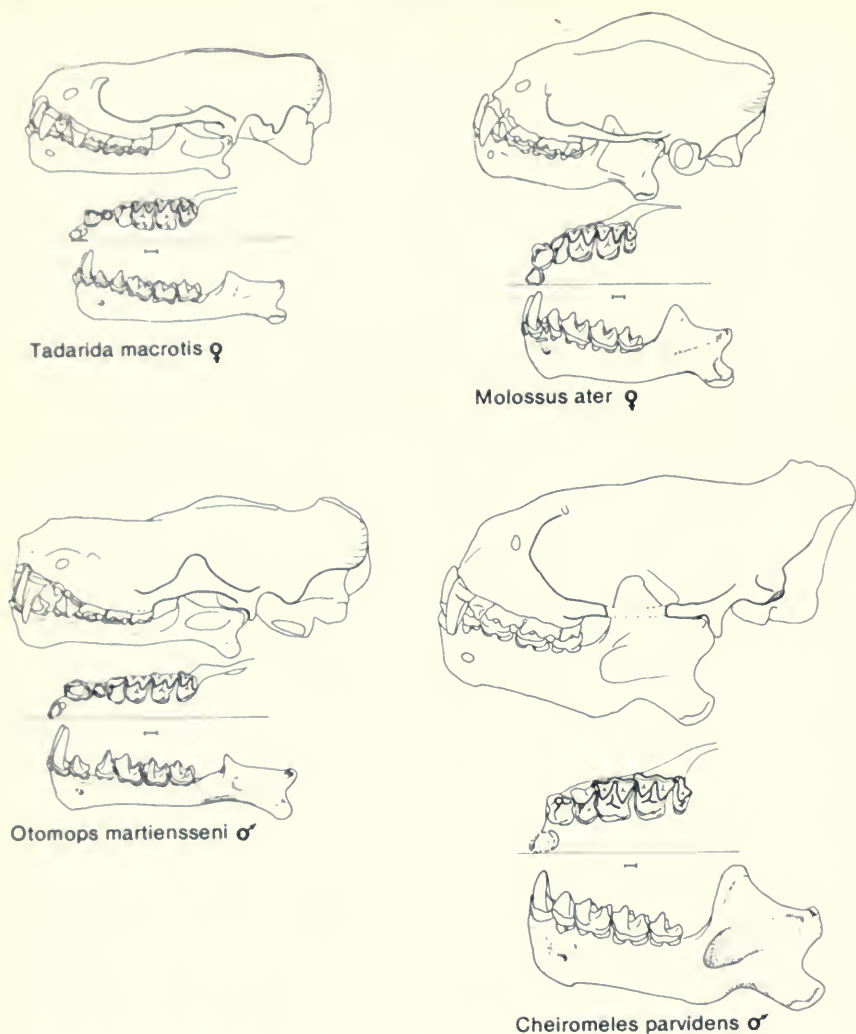
Fig. 5. Four molossids which are opposite extremes on PC II. Shown are the left lateral view of skull, occlusal view of right upper toothrow, and·lateral view of left mandible. *Tadarida macrotis* and *Molossus ater* are New World species; *Otomops martiensseni* and *Cheiromeles parvidens* are Old World species.

teeth to upper teeth takes a more dorso-anteriad direction rather than a strictly dorsal approach which occurs in those animals where the condyle is in line with the toothrow. Storch (1968) claimed this angle of attack "produced a better rendering of the food." Whatever the advantage of the elevated condyle, apparently bats with the thickest jaws, as well as the smallest bats, share the condition. Perhaps the hard exoskeleton of a beetle is best processed by the bats with elevated mandibular condyles.
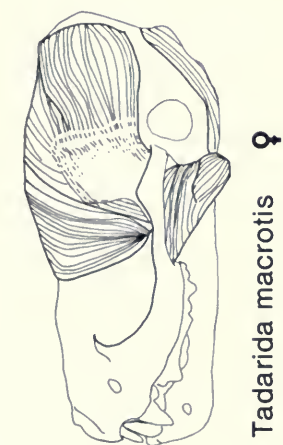
Tadarida macrotis ♀
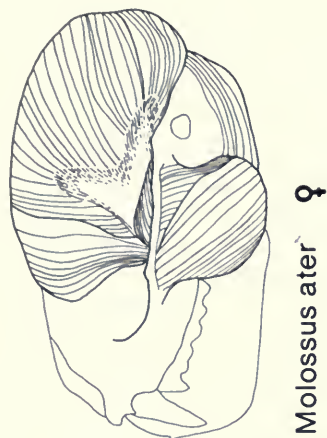
Molossus ater ♀
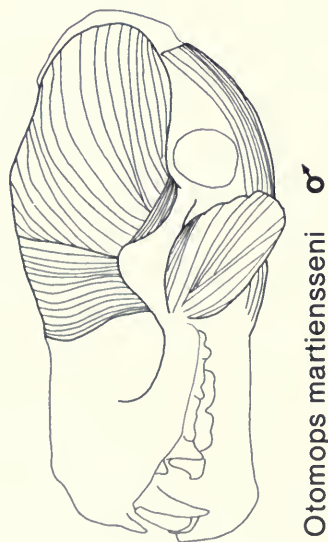
Otomops martiensseni ♂
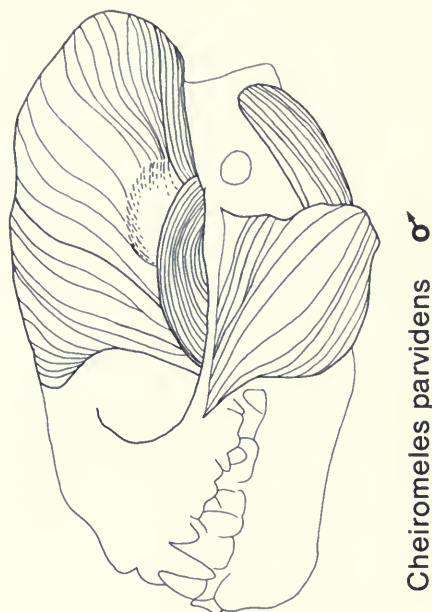
Cheiromeles parvidens ♂

FIG. 6. Jaw muscles of the same four molossids shown in Figure 5.
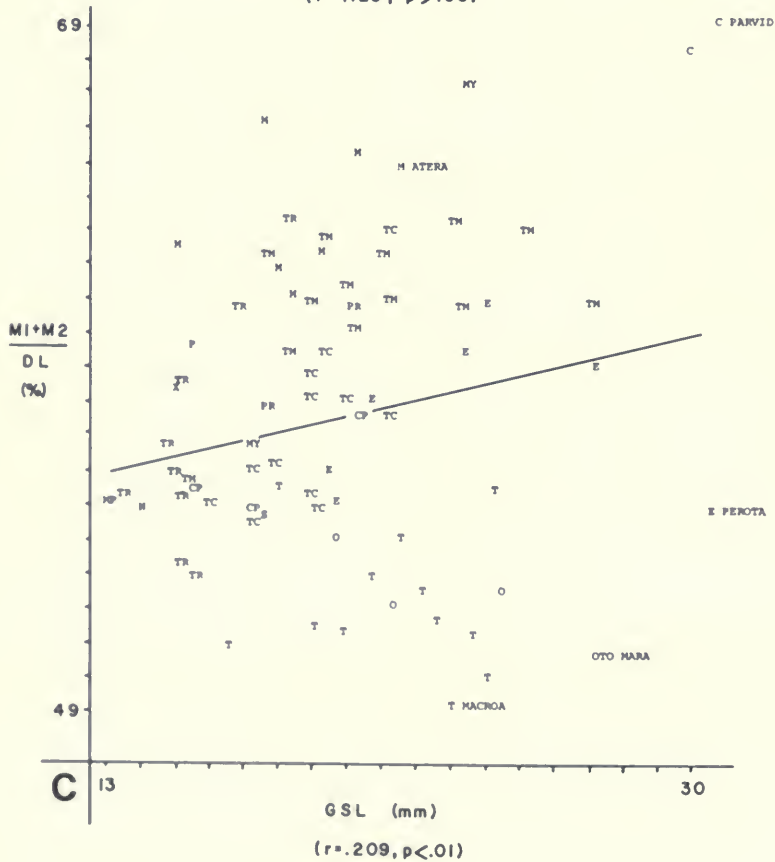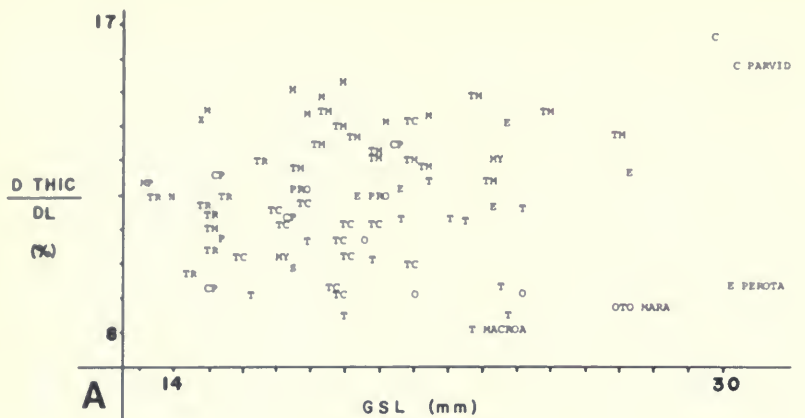
FIGURE 7.
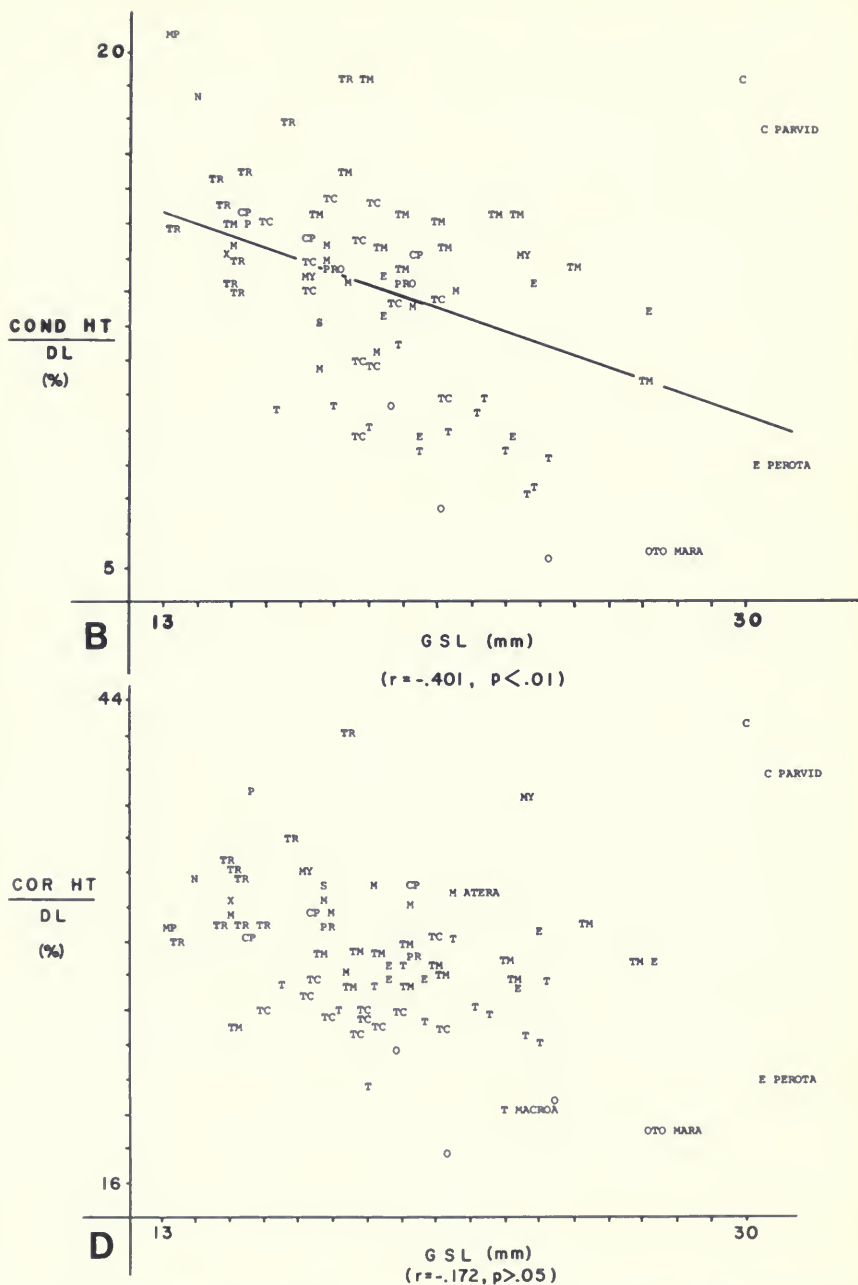
FIG. 7. Regressions of four highly correlated jaw ratios with greatest skull length, a character representing general size. The fact that **A, C,** and **D** are not statistically significant is important; that is, relative dentary thickness, moment arm index, and coronoid height do not increase as size increases. **A,** Relative dentary thickness; **B,** relative condylar height; **C,** moment arm index; **D,** relative coronoid height.

31

Modifications of upper toothrows which follow the thick-thin jaw axis have to do with loss of teeth and the general enlargement of the teeth in the toothrow (fig. 5). *Molossus ater* has lost PM^3 and the posteriormost commissure on M^3 (giving the molar a V-shaped cusp pattern), whereas *Tadarida macrotis* has retained PM^3 and the commissure on M^3 (giving the molar an N-shaped cusp pattern). Although the toothrows of the two bats are about the same length, the teeth are larger in *M. ater*, and the total length of the cusps is greater in *M. ater* (table 3). As a result, the thick-jawed *M. ater* appears to have a toothrow, posterior to the canine, of exclusively shearing edges very closely packed together, whereas *T. macrotis*, with its thin dentary, retains PM^3 and a more generalized chewing surface. The fact that species of *Molossus* have lost shearing edges from their M^3 may be the accommodation for shortening the snout and bringing the toothrow more directly beneath the powerful jaw muscles. The Old World extremes show the same trends.

There are also reductions in the numbers of lower incisors. Corresponding increase in the cingula of the lower canines is related to this loss. *Molossus ater* has only two incisors, *Tadarida macrotis* has four, and *Tadarida brasiliensis* has six, the primitive number (Allen, 1939, p. 162). Incisors in the thin-jawed bats protrude from the dentary more than those in the *Molossus* types, but what function protrusion and increased number of incisors may mean is unknown, although both may have to do with nipping or plucking. The two lower incisors in *Molossus* are virtually nonfunctional.

Gape of the jaws is a character hard to measure on most mammals, although Herring & Herring (1974) have attempted such measurements with trigonometric manipulations. Two jaw characteristics related to gape are the elevation of the condyle above the toothrow and the height of the coronoid process. The low position of the condyle in carnivores is related to having a wide gape and a powerful bite (Maynard Smith & Savage, 1959; Crompton & Heiimäe, 1969). Supposedly, the animal with the lower coronoid process can open its jaw wider without having that process run into the eye socket (Vaughan, 1972). *Tadarida macrotis* and species of *Otomops*, thin-jawed bats, should have a very wide gape, a feature which would be helpful in taking large insects. I have captured *T. macrotis* alive and found that it does, indeed, have a wide gape.

The third principal component generally separates the bats into two large

TABLE 3. Comparison of upper toothrow characteristics in five molossids which are opposite extremes on the second principal component.

Species	Sum cusps M^3-P^4 (mm.)	Sum tooth areas M^3-P^4 (mm.^{2})	MTR/ GSL (%)	Cusp row/ MTR (%)	Tooth areas/ MTR^2 (%)
T MACROA	15.2	15.1	36.5	1.8	.21
OTO MARA	15.8	18.5	37.5	1.5	.18
E PEROTA	20.8	34.7	38.6	1.7	.25
M ATERA	17.2	20.4	36.7	2.2	.30
C PARVID	22.5	35.9	34.6	2.1	.32

groups (fig. 4A). Those with large, anteriorly directed ears which join above the nose and deep basisphenoid pits are on one end, whereas those with widely separated, more laterally directed ears and shallow basisphenoid pits are on the other end. A character that covaries with these traits is the degree of wrinkling of the lips as a measure of expandability of the lips. Those species with very expandable lips (either with deep wrinkles or many fine ones) are also the bats with ears joined over the nose and deep basisphenoid pits. The bats opposite these have no wrinkles and less expandable lips.

I believe these third component features point to two basically different ways in which molossids feed. Peterson (1969) and Valdivieso et al. (1979) think the deep basisphenoid pits are related to the echolocating abilities of the bat. Deep basisphenoid pits, along with the large anteriorly directed ears, and expandable lips could mean that a bat has the ability to detect and capture single, large prey. Most of the bats having these attributes, in addition to their more gracile skull and jaws, I suspect of eating soft-bodied creatures like moths. The low coronoid process and low condyle fit neatly into this pattern, because such features would allow a large gape of the jaw, a characteristic probably important in taking large but soft prey.

Bats at the opposite extreme feed in a different way, probably detecting prey differently with their smaller, laterally directed ears and shallow basisphenoid pits. Once detected, I think prey are handled differently, perhaps more swiftly. With fewer or no wrinkles on the lips, these bats may not manipulate prey as well, but because of a higher coronoid and an elevated condyle, they may consume hard or soft-shelled prey faster and more forcefully.

The wrinkling on the lips of many molossids has been the subject of some speculation. Vaughan (1966) suggested that molossids with such lips may fly through the air with their mouths open and lips flaring like a funnel to catch many little insects. Maybe, but I think the wrinkles mean the lips are expandable and aid in the manipulation of prey items. *Tadarida macrotis* has deeply wrinkled lips. When fed several mealworms in succession, this bat does not appear to chew each one and swallow it, but keeps all of them in its lips and cheeks until they are bulging and then processes the whole mass. Not all expandable lips are marked by deep wrinkles; some are skirtlike in appearance and have fine, microscopic wrinkles. *Eumops perotis* is one of this latter variety, along with species of *Otomops* and the large African *Tadarida*. I have seen *Eumops perotis* feeding on crickets. The lips are prehensile and hold the inedible parts, like the femora and head, which are snipped off while the rest of the cricket is consumed. Finally the inedible parts, which have remained in the lips or cheeks, are spit out. That these bats have the ability to hold and manipulate prey with the lips while flying seems a reasonable speculation. It would be interesting to see how a bat on the opposite end of the axis catches and handles prey. Also, the wrinkled lips may be related to how the bat emits sounds, as molossids are known to be oral sound emitters.

The fourth principal component indicates that a wing character, the second phalanx of digit IV, is an important character of variation among molossids. In comparison with other wing characters—such as the indices of Findley et al. (1972), aspect ratio and tip index, or the wing index of Fenton (1972), metacarpal III/metacarpal V—the relative length of the phalanx of the total length of digit IV is far more variable (table 4). Although the three indices mentioned are distinctive for the family, they tell nothing of the variation within the family. The

TABLE 4. Comparison of selected wing characters: relative length of the second phalanx of digit IV, aspect ratio, tip index, and digit III/digit V ratio (aspect ratio and tip index are taken after Findley et al., 1972; digit III/digit V ratio, after Fenton, 1972). Species are arranged by genus and are ordered according to increasing relative length of the second phalanx of digit IV.

Tadarida

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
T MACROA	3.10	2.94	64.93	1.90
T FEMORA	3.70	2.96	66.79	1.98
T AURISA	3.75	2.91	66.69	1.94
T LATICA	4.25	2.86	65.35	1.87
T AFRICA	9.16	2.78	65.80	1.83
T FULMIN	9.28	2.92	65.57	1.91
T LOBATA	10.66	2.72	66.44	1.81
T AEGYPA	11.23	2.83	65.70	1.86
T TENIOA	12.00	2.86	66.05	1.89
T BRASIA	12.67	2.79	65.65	1.83
T ANSORA	14.53	2.90	66.88	1.94
T KUBORI	17.14	2.97	66.28	1.97
T AUSTRA	17.35	2.85	66.21	1.88

Chaerephon

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
TC ALOYA	14.40	2.94	66.54	1.96
TC BIVIA	14.40	2.93	66.91	1.96
TC RUSSA	14.84	2.92	67.58	1.98
TC PLICA	15.58	2.82	66.20	1.87
TC BEMMI	15.59	2.85	66.90	1.91
TC JOHOR	15.71	3.03	66.74	2.02
TC MAJOR	16.52	2.88	66.50	1.92
TC JOBEN	16.58	2.97	66.71	1.98
TC NIGEA	17.03	2.84	67.23	1.91
TC PUMIA	17.68	2.72	67.41	1.84
TC CHAPI	17.72	2.86	66.10	1.89

Mops

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
TM CONGA	12.24	2.97	67.80	2.01
TM NIANG	13.80	2.98	67.23	2.01
TM TREVO	13.92	2.98	67.65	2.02
TM LEONA	15.00	2.71	66.00	1.79
TM SARSA	15.09	3.02	66.42	2.00
TM MOPSA	15.77	2.87	65.80	1.89
XIPHONYC	16.70	2.76	65.11	1.80
TM NANUA	16.81	2.85	66.36	1.83
TM MIDAA	16.88	2.85	66.85	1.91
TM NIVEI	17.26	2.87	67.00	1.92
TM DEMOA	17.40	2.72	66.95	1.82
TM BRACH	17.44	2.80	68.31	1.92
TM THERA	17.93	2.84	67.28	1.91
TM CONDA	19.77	2.82	68.58	1.93

Mormopterus-Sauromys-Platymops

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
TR PHRUD	9.40	2.63	64.96	1.71
TR KALIN	13.26	2.71	64.46	1.75
TR MINUA	14.19	2.53	65.64	1.66
TR JUGUA	15.74	2.84	64.51	1.83
TR BECCR	15.80	2.77	66.28	1.83
TR ACETA	16.12	2.48	65.19	1.61
TR PLANA	18.21	2.65	67.00	1.78
TR LORIA	18.59	2.61	68.35	1.79
TR NORFA	18.75	2.67	66.84	1.78
SAUROMYS	11.39	2.56	66.11	1.69
PLATYMOP	17.40	2.42	66.67	1.61

length of the second phalanx varies between 3 and 20 per cent of the total length of the fourth digit. All molossids are thought to be fast fliers (Vaughan, 1959, 1966; Hartman, 1963; Struhsaker, 1961; Findley et al., 1972; Fenton, 1972), and are correspondingly set apart from other bat families. Variability in the last phalanx of digit IV may mean that, although molossids are fast, there is further gradation in the degree of swiftness and maneuverability within the already fast-flying family. I believe short length in this character is related to a narrow wing tip, resulting in faster, less maneuverable flight, whereas the long phalanx means a broader tip, more camber, more maneuverability, and possibly less speed. Bats with the narrow tips should fly in more open areas, and those with broad tips should be in areas with more obstacles, trees of a forest or possibly walls of a cave.

TABLE 4. *Continued.*

Conglomerate-Cheiromeles

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
CP GREEA	6.87	2.86	66.40	1.90
CP BRACA	7.49	2.87	67.96	1.95
CP PLANA	8.50	2.83	67.15	1.90
NEOPLATA	12.34	2.48	65.75	1.63
MYOP WHA	17.10	2.64	66.91	1.77
MYOP ALB	17.20	2.70	67.08	1.80
MP TEMMA	19.92	2.50	67.02	1.68
C PARVID	16.60	3.13	70.23	2.20
C TORQUT	17.12	3.14	69.95	2.19

Eumops

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
E HANSAA	5.54	3.01	65.11	1.96
E PEROTA	5.73	2.88	68.41	1.92
E GLAUCA	6.40	2.94	66.43	1.95
E BONARA	6.59	2.70	66.90	1.81
E AURIPA	6.90	3.04	67.43	2.05
E UNDERA	7.14	2.87	67.79	1.95
E MAURUS	7.80	2.93	66.54	1.95

Molossus

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
M PRETIA	4.50	3.00	65.82	1.97
M COIBEA	4.60	2.90	67.34	1.95
M BONDAA	4.80	2.86	66.86	1.91
M ATERA	4.84	2.85	66.36	1.89
M MOLOSS	5.40	2.79	66.61	1.86
M SINALA	5.60	2.81	65.90	1.85
M TRINIT	6.10	2.82	66.82	1.88

Otomops-Promops-Vespertilionids

	4M 2PHAL DIGIT IV	ASPECT	TIP INDX	D3/D5
OTO SECA	11.50	2.99	64.54	1.93
OTO PAPU	12.60	2.90	64.96	1.88
OTO MARA	12.95	2.85	65.19	1.86
OTO WROA	13.20	2.89	65.32	1.89
PRO NASU	4.30	2.64	67.03	1.78
PRO CENA	4.40	2.82	67.21	1.90
MIMETILL	4.46	2.41	62.23	1.50
NYCTALUS	9.30	2.64	65.24	1.72

The functional significance of size in these bats has several obvious ramifications. Larger bats probably take larger prey and require larger places to roost, whereas smaller bats take smaller items and can live in smaller roosting places. A size difference between males and females of the same species is common, with the males usually being larger. Besides size, males have larger canines and larger cranial crests, but why these sexually dimorphic differences occur has not yet been determined.

Certain patterns, however, appear among small bats alone or large bats alone. For example, some of the smaller bats seem to feed on both hard and soft items whether they have thick or thin jaws. Thompson (1971) mentioned that smaller animals are stronger, proportionally, than larger ones because muscle power varies by the square of linear dimensions, whereas volume varies by the cube. Also, patterns in tooth loss and jaw structure and wing configuration in the smaller bats are discussed in the sections concerned with the morphological features of the groups.

Large congeners are thought to be allometric with respect to small congeners. That is, they are out of proportion with the smaller animal and are not merely photographic, or isometric, enlargements of that shape. Several groups of molossids appear to have a more predictable allometric relationship between small and large congeners. In *Mops* and *Molossus*, size seems to be the only thing which separates the species, and shape seems to change very little. These

genera are also two which have lost teeth and cusps and are suspected of concentrating on hard-shelled food items.

MORPHOMETRIC DESCRIPTIONS OF GROUPS

Placement of the 80 OTU's onto the principal components is illustrated in Figure 4 where components II, III, and IV, only, are shown. Component I, which is size-related, has been omitted. Starting with the more compact clusters of bats, I discuss each OTU with respect to: 1) position in the PCA; 2) relationships in the three clustering analyses (distance, size-in and size-out, and correlation); 3) size and functional interpretations; 4) possible ecological capabilities; and 5) natural history support or nonsupport for the predictions made by the analysis.

Several of the classical genera or subgenera form distinct clusters in this analysis. Results of my study often substantiate and quantify classical observation. Until I restrict it further, I use the name *Tadarida* to mean what is now *Tadarida* (*Tadarida*), including both Old and New World species. Only if *Tadarida* (*sensu lato*) is used does the name include all subgenera of *Tadarida*. Likewise, I treat *Chaerephon*, *Mops*, and *Mormopterus* as genera, not subgenera, of *Tadarida*.

In the three space components II, III, and IV, several groups appear as compact entities. These groups are *Cheiromeles*, *Molossus*, *Mops*, *Chaerephon*, and finally, a group of three species of *Otomops* plus *Tadarida macrotis*. The remaining bats form no distinctly isolated clusters. The least compact group of species, supposedly belonging to a single taxon, are species of the genus *Eumops*. Average least distances among species within classical taxa or groups formed by this study quantify the dispersion in each (table 5). I arbitrarily designate the mean least distance of the two distance matrices (size-in and size-out) as the dividing points below which taxa are considered compact and above which taxa are considered dispersed. Although five of the groups which form compact clusters on the PCA are also considered compact in table 5 (*Cheiromeles*, *Molossus*, *Mops*, *Chaerephon*, and *Otomops*), there are several other compact groups derived from the distance matrix which do not appear as distinct entities on the PCA (*Cynomops*, *Promops*, and *Mormopterus*). The PCA gives an overview of the phenetic resemblance of all the bats; distance and correlation determine the closest morphological neighbors of each species. All of the groups (genera and subgenera) I use in the following morphological analysis have nearest neighbors within the group. The phenogram of the size-out distance matrix presented in the final section on evolution summarizes the phenetic relatedness of all the species in the groups. The groups I use here are mostly classical taxa and are convenient for explanation. In the final section, I modify these groups into what I think are the natural genera of the family.

I use the size-out distance matrix extensively to quantify what can be seen in the three- and two-dimensional plots representing the PCA (fig. 4). Nearest neighbors within a taxon (genus or subgenus) can be taken from the matrix, but nearest neighbors among taxa have a more complicated derivation (fig. 8). As an example, taxon J has three species, a, b, and c; and taxon K has three species, d, e, and f. The distance from a to d, e, and f can be obtained and averaged as can that from b to d, e, and f; and c to d, e, and f. In turn, a's average distance to K, b's average distance to K, and c's average distance to K can all three be summed together and averaged. The result is the average distance from J to K or

TABLE 5. Average least distances of members within a taxon for both size-in and size-out distance (averages below the mean of each matrix are considered compact; those above, dispersed).

SIZE-OUT		SIZE-IN	
Cheiromeles	.278	Cheiromeles	.301
Cynomops	.304	Molossus	.437
Promops	.313	Mormopterus	.437
Molossus	.328	Chaerephon	.441
Mops	.385	Mops	.458
Otomops	.390	Mormopterus	.475
Chaerephon	.364	Sauromys	
Mormopterus	.384	Platymops	
Mormopterus	.416	Molossops	.492
Sauromys		Neoplatymops	
Platymops			
Mean least distance of matrix	.420	Mean least distance of matrix	.508
Molossops	.423	Otomops	.535
Neoplatymops		Promops	.559
Cynomops		Tadarida	.562
New World Tadarida (excl. T BRASIA)	.443	Cynomops	.570
Old and New World Tadarida	.458	Eumops	.607
Old World Tadarida (incl. T BRASIA)	.464	Myopterus	1.489
Molossops Neoplatymops	.491		
Myopterus	.528		
Eumops	.560		

the average distance between supraspecific taxa. If the average distance, J to K, is the smallest average distance value of J to any other taxon, then the J-K value is the least average, and K is J's nearest neighboring taxon. From these values, least and greatest averages, or nearest and farthest neighbors, for each genus or subgenus are taken.

Molossus

Molossus is a genus of New World bats that is found mostly south of the Tropic of Cancer and here includes the species *M. ater*, *M. bondae*, *M. coibensis*, *M. molossus*, *M. sinaloae*, *M. pretiosus*, and *M. trinitatus*. Species of the genus are distinctly clustered and isolated from other bats in the PCA (fig. 4) and tend to be extreme on the shape-related components. Members of the genus *Molossus* have a heavy build, mastiff appearance, thick jaws, and narrow wing tips. Their

$\bar{a}$ to K

$\bar{b}$ to K

$\bar{c}$ to K

___

$\bar{\bar{x}}$ to K
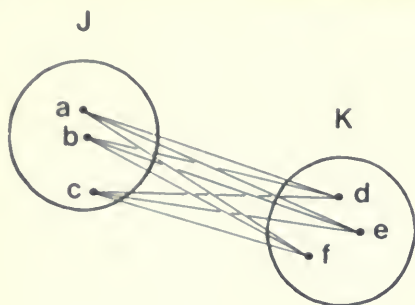
FIG. 8. Diagrammatic scheme of calculating the average distance among taxa. Taxa are J and K; species are a, b, c, d, e, and f; and $\bar{\bar{x}}$ is the average distance from J to K. If $\bar{\bar{x}}$ is the smallest distance value of J to any other taxa, then $\bar{\bar{x}}$ is the least average distance and K is the nearest taxa to J.

ears are neither completely separated nor fully joined over the nose. Average relative dentary thickness is 14 per cent of dentary length, whereas the average percentage that the second phalanx comprises of digit IV is 5 per cent (table 6). Other jaw-related characters include: well-developed sagittal and lambdoidal crests and coronoid process, condyle well above the toothrow (the mean is 13 per cent of dentary length), diminution of the last upper molar (V-shape), and absence of the third upper premolar (fig. 9, appendix A).

Molossus trinitatus, a slightly outlying species on axis II, is not as robust as other *Molossus* in some jaw and skull features, such as relative coronoid height and development of sagittal and lambdoidal crests. *Eumops auripendulus*, a very robust species, is close to the *Molossus* cluster on the PCA (fig. 4). I treat it as a *Molossus*-like *Eumops* rather than as a *Eumops*-like *Molossus* and discuss it in the *Eumops* section.

There is no species of *Molossus* that is not a nearest neighbor to or most highly correlated with a congener in the three clustering methods (table 7). The genus is a very compact group in the family and has a relatively small average least distance (size-out) among its species (0.328), well below the point demarcating compact and dispersed groups. *Molossus* is a compact group even when size is included (0.437), being second only to *Cheiromeles* (table 5).

As for nearest neighbors among taxa (table 8), the nearest genus to *Molossus* is *Promops* (0.687), whereas the farthest genus is *Otomops* (1.331). These near and far genera correspond well with the placement of the three genera in the PCA.

Greatest skull length among the seven species of *Molossus* dealt with here ranges from 15.0 mm in *M. coibensis* to 21.5 mm in *M. ater* (table 1). There are no extremely small or large *Molossus*. There seem to be few changes in shape among species as the species get larger, and I suspect the allometric relationship between small and large congeners is more predictable than that in other genera.

TABLE 6. Six important characters (in percentages) as indicated by the PCA and ordered from least to greatest (*Mormopterus* and Conglomerate contain the same taxa as listed in Table 1).

Relative dentary thickness (DYTHIC/DL)

Tadarida	Chaerephon	Mops	Mormopterus	Conglomerate	Eumops	Molossus	Otomops	Promops
T MACROA 8.2	TC NIGRA 9.1	TM MANUA 11.1	TR KALIN 9.3	MYOP WRA 10.2	E PEROTA 9.2	M PRETIA 13.9	OTO MARA 8.6	PRO CEMA 11.8
T TENIOA 8.2	TC ALOYA 9.9	TM TREVO 12.3	TR ACETA 9.6	CP GREZA 11.3	E BONARA 10.1	M ATERA 14.1	OTO SECA 9.0	PRO NASU 12.1
T FEMORA 8.3	TC CHAPI 10.0	TM LEONA 12.6	SAURONYS 9.7	NEOPLATA 11.8	E GLAUCA 11.6	M BORIDAA 14.3	OTO WROA 9.0	
T BRASIA 8.8	TC JOMOR 10.1	TM MOPSA 12.8	TR PLANA 10.3	MP TEMMA 12.2	E HANSBA 11.9	M COIBEA 14.3	OTO PAPU 10.5	
T ANBORA 9.3	TC RUSSA 10.5	TM NIVEI 12.8	PLATYNOP 10.5	CP PLANA 12.5	E MAURUS 12.2	M TRINIT 14.7		
T AUSTRA 9.3	TC PLICA 10.9	TM DEMOA 12.9	TR NORFA 11.3	MYOP ALB 12.9	E UNDERA 12.4	M MOLOSS 14.9		
T AEGYPA 10.0	TC BIVIA 11.0	TM CONDA 13.0	TR LORIA 11.5	C BRACA 13.2	E AURIPA 13.9	M SINALA 15.0		
T LATICA 10.5	TC PUMIA 11.2	TM BRACH 13.3	TR MINUA 11.7	C PARVID 15.5				
T AURISA 11.1	TC MAJOR 11.4	TM SANBA 13.4	TR PHNUD 11.8	C TORQUT 16.4				
T LOBATA 11.1	TC BEMMI 11.6	TM MIDAA 13.5	TR JUGUA 12.8					
T FULAIN 11.2	TC JOBEN 14.0	TM THERA 13.8	TR BECCR 14.5					
T AFRICA 11.4		XIPHONYC 14.2						
T KUBORI 12.6		TM CONGA 14.3						
		TM NIANG 14.7						

Relative condylar height (CONHT/DL)

Tadarida	Chaerephon	Mops	Mormopterus	Conglomerate	Eumops	Molossus	Otomops	Promops
T AUSTRA 7.0	TC RUSSA 8.9	TM MIDAA 10.4	SAURONYS 12.1	MYOP WRA 13.6	E PEROTA 7.9	M MOLOSS 10.7	OTO WROA 5.1	PRO CEMA 13.2
T TENIOA 7.1	TC ALOYA 9.9	TM DEMOA 13.6	TR PLANA 13.1	CP BRACA 13.9	E GLAUCA 8.7	M SINALA 11.3	OTO MARA 5.4	PRO NASU 13.8
T AFRICA 8.0	TC PLICA 10.9	TM CONGA 13.7	TR NORFA 13.2	MYOP ALB 14.0	E MAURUS 8.8	M PRETIA 12.5	OTO SECA 6.7	
T MACROA 8.2	TC BIVIA 12.5	TM MOPSA 14.2	TR KALIN 14.0	CP GREZA 14.5	E BONARA 12.3	M ATERA 12.8	OTO PAPU 9.7	
T AURISA 8.3	TC JOBEN 13.0	TM SANBA 14.2	TR MINUT 14.9	CP PLANA 15.2	E UNDERA 12.4	M TRINIT 13.2		
T KUBORI 8.8	TC MAJOR 13.0	XIPHONYC 14.2	PLATYNOP 14.9	C PARVID 17.7	E AURIPA 13.3	M BORDAA 14.3		
T FEMORA 9.1	TC PUMIA 13.8	TM MANUA 14.8	TR LORIA 15.4	NEOPLATA 18.6	E HANSAA 13.4	M COIBEA 14.3		
T FULAIN 9.4	TC NIGRA 14.4	TM NIVEI 14.9	TR ACETA 16.3	C TORQUT 19.1				
T BRASIA 9.6	TC CHAPI 15.0	TM LEONA 15.1	TR PHNUD 16.4	MP TEMMA 20.4				
T LATICA 9.7	TC JOMOR 15.5	TM CONDA 15.2	TR JUGUA 17.9					
T LOBATA 9.9	TC BEMMI 15.7	TM NIANG 15.3	TR BECCR 19.1					
T ANBORA 10.9		TM TREVO 15.3						
T AEGYPA 11.4		TM BRACH 16.4						
		TM THERA 19.2						

TABLE 6. Continued.

Moment arm index (AI+M2/BL)

Tedarida	Chaerephon	Mops	Mormopterus	Conglomerate	Eumops	Molossus	Otomops	Promops
T MACROA 49.1	TC MAJOR 54.5	TM MANUA 55.6	TR PHNUD 52.7	CP GREEA 54.8	E PEROTA 54.8	M TRINIT 61.2	OTO MARA 50.5	PRO MASU 57.8
T TENICA 50.0	TC CHAPI 55.0	XIPHONYC 58.5	TR KALIN 53.3	NEOPLATA 55.1	E BONBUA 55.1	M BONDAA 61.9	OTO BECA 52.2	PRO CENA 60.3
T BRASIA 50.9	TC JOHOB 55.0	TM BRACH 59.4	SAUKOMYS 54.8	MP TERMA 55.1	B KANBAA 56.0	M SINALA 62.4	OTO WROA 52.6	
T AUSTRA 51.3	TC NIGRA 55.3	TM CONDA 60.1	TR PLANA 55.1	CP PLANA 55.4	E MAURUS 58.1	M COIBRA 62.5	OTO PAPU 54.0	
T ABGTPA 51.4	TC PUMIA 56.0	TM TREVO 60.8	TR MINUA 55.3	MTOP MNA 56.8	E UNGERA 59.0	M ATERA 64.7		
T PENOBA 51.5	TC BEMMI 56.2	TM THERA 60.8	TR LORIA 55.8	CP BRACA 57.6	E GLAUCA 59.5	M PRETIA 65.3		
T LOBATA 51.9	TC ALOTA 57.7	TM MIDAA 60.9	TR ACETA 56.7	MTOP ALB 67.3	E AURLPA 60.7	M MOLOSS 66.1		
T FULMIN 52.5	TC BIVIA 58.1	TM MOPSA 61.0	TR MORFA 58.5	C TORQUT 68.2				
T AURISA 52.8	TC RUSSA 58.9	TM DEMCA 61.4	PLATYMOP 59.6	C PANVID 69.0				
T KUBORI 54.1	TC PLICA 59.4	TM LEONA 62.2	TR JUGUA 60.7					
T AFRICA 55.4	TC JOBEN 62.9	TM NIVEI 62.2	TR BECCR 63.4					
T LATICA 55.6		TM SABBA 62.7						
T ANSORA 58.1		TM CONGA 62.9						
		TM NIANG 63.2						

Relative coronoid height (COR H/BL)

Tedarida	Chaerephon	Mops	Mormopterus	Conglomerate	Eumops	Molossus	Otomops	Promops
T MACROA 20.1	TC ALOTA 24.6	TM MANUA 25.0	TR MINUA 29.6	CP PLANA 30.4	E PEROTA 22.8	M TRINIT 27.9	OTO BECA 17.9	PRO CENA 28.7
T PENOBA 21.2	TC PLICA 25.0	TM DEMCA 27.1	TR ACETA 30.8	MP TERMA 30.6	E GLAUCA 27.2	M COIBRA 31.3	OTO MARA 18.8	PRO MASU 31.0
T TENICA 24.1	TC BEMMI 25.6	TM BRACH 27.3	TR KALIN 30.8	CP GREEA 31.5	E BONBUA 27.5	M BONDAA 31.7	OTO WROA 20.5	
T AUSTRA 24.4	TC BIVIA 25.7	TM TREVO 27.6	TR PHNUD 30.9	CP BRACA 33.1	E MAURUS 27.7	M PRETIA 31.9	OTO PAPU 23.4	
T ANSORG 24.8	TC NIGRA 25.8	TM MOPSA 28.4	SAUKOMYS 33.1	NEOPLATA 33.3	E KANBAA 28.4	M MOLOSS 32.2		
T AURIKA 25.0	TC RUSSA 25.8	TM NIVEI 28.4	TR PLANA 33.6	MTOP MNA 33.9	E UNGERA 28.6	M ATERA 32.7		
T LATICA 25.8	TC CHAPI 26.0	TM MIDAA 28.6	TR MORFA 34.0	MTOP ALB 38.6	E AURLPA 30.6	M SINALA 33.1		
T LOBATA 25.9	TC MAJOR 26.8	TM MIANG 28.8	TR LORIA 34.6	C PANVID 39.8				
T FULMIN 26.2	TC JOHOR 27.1	TM EABBA 29.1	TR JUGUA 35.9	C TORQUT 42.7				
T BRASIA 27.2	TC PUMIA 27.6	TM THERA 29.2	PLATYMOP 38.6					
T AFRICA 27.4	TC JOBEN 30.1	TM LEONA 29.4	TR BECCR 42.0					
T ABGTPA 28.6		TM CONDA 29.7						
T KUBORI 30.2		TM CONGA 30.9						
		XIPHONYC 32.1						

TABLE 6. Continued.

Relative length of second phalanx of digit IV (4M 2PHAL/DIGIT 4)

Tadarida	Chaerephon	Mops	Mormopterus	Conglomerate	Eumops	Molossus	Otomops	Promops
T MACROA 3.1	TC ALOYA 14.4	TM CONGA 12.2	TR PHRUD 9.4	CP GREZA 6.9	E HANSAA 5.5	M PRETIA 4.5	OTO SECA 11.5	PRO NASU 4.3
T FEMORA 3.7	TC BIVIA 14.4	TM NIANG 13.8	SAUROMYS 11.4	CP PLANA 7.5	E PEROTA 5.7	M COIBEA 4.6	OTO PAPU 12.6	PRO CENA 4.4
T AURISA 3.8	TC RUSSA 14.8	TM TREVO 13.9	TR KALIN 13.3	CP BRACA 8.5	E GLAUCA 6.4	M BONDAA 4.8	OTO MARA 13.0	
T LATICA 4.2	TC PLICA 15.6	TM LEONA 15.0	TR MINUA 14.2	NEOPLATA 12.3	E BONARA 6.6	M ATERA 4.8	OTO WROA 13.2	
T AFRICA 9.2	TC BEMMI 15.6	TM SARSA 15.9	TR JUGUL 15.7	C PARVID 16.6	E AURIPA 6.9	M MOLOSS 5.4		
T FULMIN 9.3	TC JOMOR 15.7	TM MOPSA 15.8	TR BECCR 15.8	C TORQUT 17.1	E UNDERA 7.1	M SINALA 5.6		
T LOBATA 10.7	TC MAJOR 16.5	XIPHONYC 16.7	TR ACETA 16.1	MYOP WHA 17.1	E MAURUS 7.8	M TRINIT 6.1		
T AEGYPA 11.2	TC JOBEN 16.6	TM NANUA 16.8	PLATYMOP 17.4	MYOP ALB 17.2				
T TENIOA 12.0	TC NIGEA 17.0	TM MIDAA 16.9	TR PLANA 18.2	MP TEMMA 19.9				
T BRASIA 12.7	TC PUMIA 17.7	TM NIVEI 17.4	TR LORIA 18.6					
T ANSORA 14.5	TC CHAPI 17.7	TM DEMOA 17.4	TR NORPA 18.8					
T KUBORI 17.1		TM BRACH 17.4						
T AUSTRA 17.4		TM THERA 17.9						
		TM CONDA 19.8						

Relative length of M³ (M3 LENG/DL)

Tadarida	Chaerephon	Mops	Mormopterus	Conglomerate	Eumops	Molossus	Otomops	Promops
T AFRICA 6.3	TC MAJOR 7.3	TM SARSA 5.2	SAUROMYS 7.3	MYOP WHA 5.1	E MAURUS 4.7	M MOLOSS 5.0	OTO MARA 8.1	PRO NASU 6.0
T LOBATA 7.4	TC BIVIA 7.4	TM DEMOA 5.7	TR BECCR 8.4	C TORQUT 5.9	E GLAUCA 5.8	M SINALA 6.0	OTO SECA 8.1	PRO CENA 7.4
T ANSORA 7.8	TC NIGEA 7.6	TM MIDAA 5.7	TR JUGUA 8.5	C PARVID 6.2	E AURIPA 6.3	M TRINIT 6.2	OTO WROA 9.0	
T AUSTRA 8.1	TC ALOYA 7.7	TM MOPSA 5.7	TR MINUA 8.5	MYOP ALB 6.4	E PEROTA 7.0	M BONDAA 6.3	OTO PAPU 9.7	
T FULMIN 8.1	TC JOBEN 7.7	XIPHONYC 5.7	TR ACETA 8.7	CP GREEA 6.4	E UNDERA 7.1	M COIBEA 6.3		
T TENIOA 8.2	TC PLICA 7.8	TM NIANG 6.1	PLATYMOP 8.8	CP BRACA 6.6	E BONARA 8.7	M PRETIA 6.3		
T AURISA 8.3	TC RUSSA 8.1	TM TREVO 6.1	TR PHRUD 9.1	CP PLANA 7.1	E HANSAA 9.0	M ATERA 6.4		
T AEGYPA 8.6	TC BEMMI 8.3	TM THERA 6.2	TR PLANA 9.3	MP TEMMA 8.1				
T BRASIA 8.8	TC PUMIA 8.6	TM CONGA 6.3	TR NORPA 9.4	NEOPLATA 8.8				
T KUBORI 8.8	TC CHAPI 9.0	TM CONDA 6.5	TR LORIA 9.6					
T MACROA 8.8	TC JOMOR 9.3	TM NANUA 6.5	TR KALIN 10.3					
T LATICA 8.9		TM LEONA 6.7						
T FEMORA 9.1		TM NIVEI 6.8						
		TM BRACH 7.0						

41

Molossus coibensis ♂
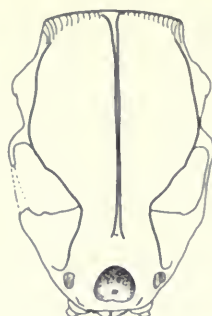
Molossus molossus ♂
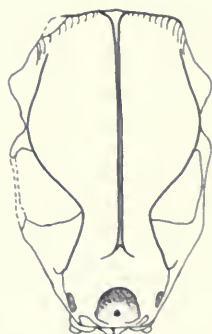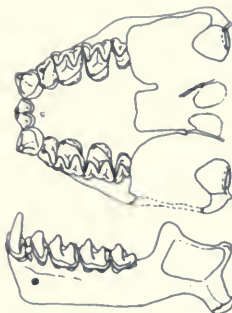
Molossus bondae ♂

FIGURE 9.

42
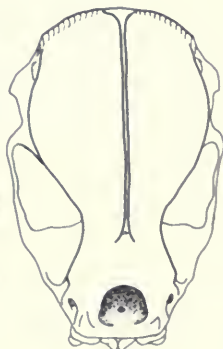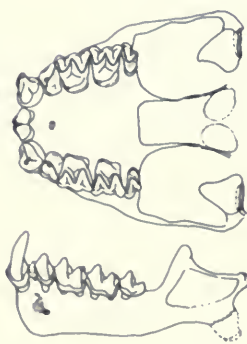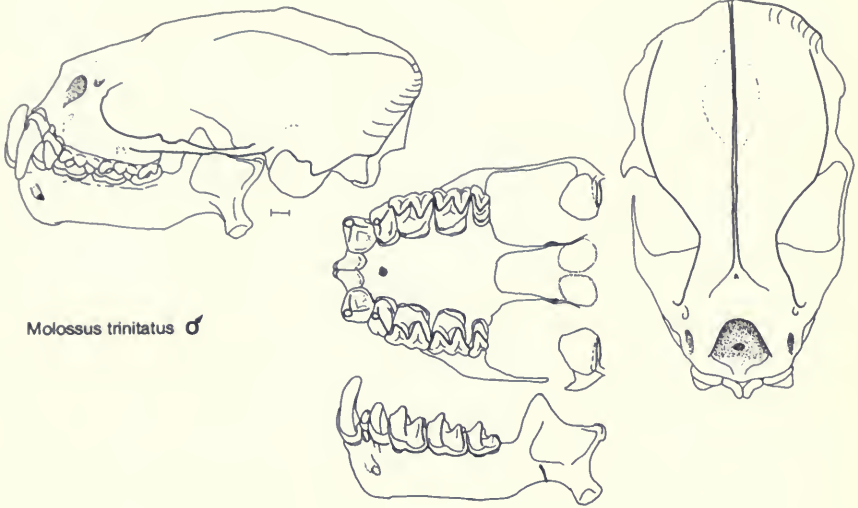
Molossus trinitatus ♂
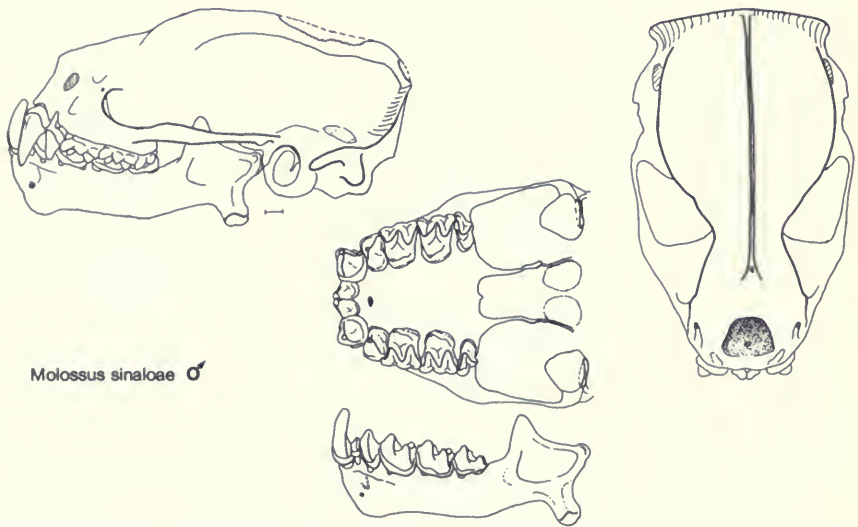
Molossus sinaloae ♂

FIGURE 9.

43
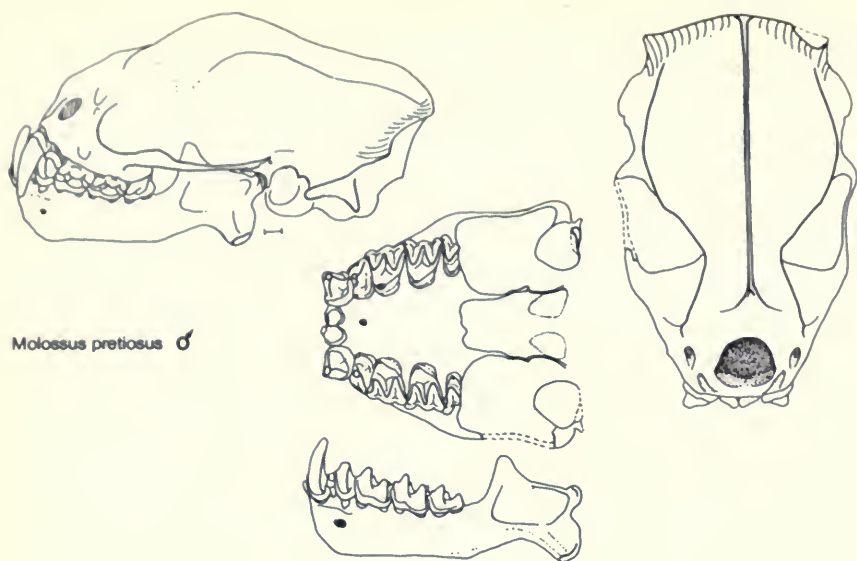
Molossus pretiosus ♂
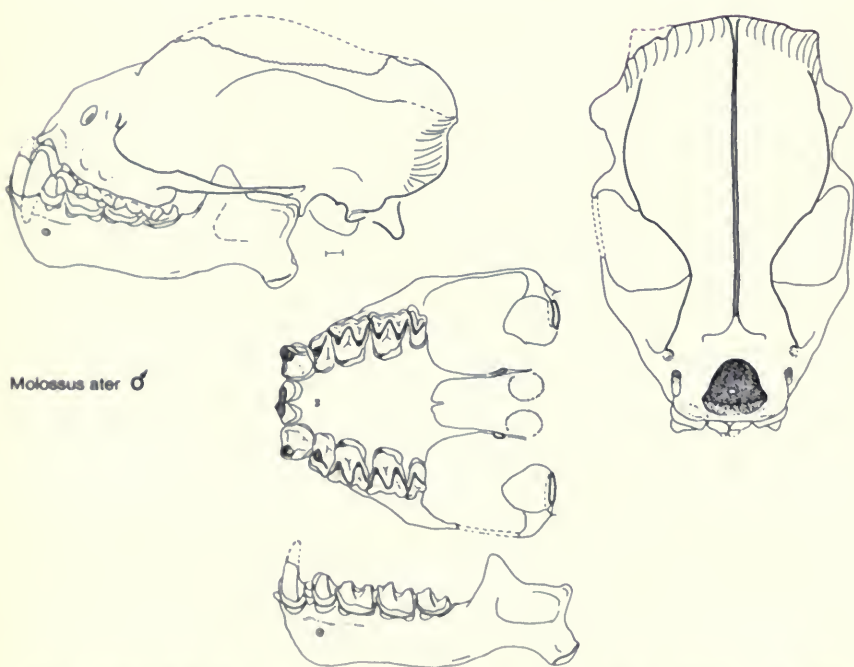
Molossus ater ♂

FIG. 9. Seven species of *Molossus* arranged from small to large. Lateral, dorsal, and occlusal views of the skulls and lateral view of the mandible are given for each.

Morphologically, the species of *Molossus* are among the most derived molossids in the sense that they have lost teeth due to the foreshortening of the jaw. More qualitative distinguishing features include an upper toothrow of broad molariform teeth with shearing edges and an upper intercanine space, not emarginate as in several other genera, but filled with two sturdy beaklike incisors. Upper toothrows of *M. ater* and *Tadarida macrotis*, bats of approximately the same size (maxillary toothrows = 7.9 and 8.4 mm, respectively; whereas MTR/GSL = 36.7 and 36.5 per cent) are illustrated in Figure 5. Proportionally and actually, the canines and molars of *M. ater* are much larger than those of *T. macrotis*, the latter having retained a rather large PM³ (table 3).

It seems ecologically reasonable that *Molossus* is capable of eating hard items such as beetles, and that it can fly very fast. Food studies done thus far support the first prediction of eating hard prey. Howell & Burch (1974) reported a large percentage by volume of beetle remains in *M. molossus* in Costa Rica (100 per cent in one and 88 per cent in eight of nine specimens) and a substantial percentage of non-moth remains in *M. ater* (50 per cent mixed Hymenoptera, Coleoptera, and Orthoptera in one specimen). Pine (1969) reported much the same in another specimen of *M. ater* with 86 per cent Hymenoptera (2–8 mm long and mostly ants) and 12 per cent Coleoptera (8–25 mm long). My own analysis of fecal samples of five Central American species of *Molossus* shows the feces to have few moth scales compared with the numbers found in some species of *Tadarida* (table 9). The samples examined have a large proportion of beetle exoskeleton in them, and only two of 15 of the small *M. coibensis* had more than a few thousand moth scales in them. Anecdotally, the strength with which a large *Molossus* can bite was communicated to me by Scott Altenbach, who said it gave him one of the worst bites he had ever suffered from a bat and that, by comparison, the bite of *T. macrotis* was mild.

Species of *Molossus* are probably fast fliers, but are capable of less maneuverable flight because their narrow wing tips would have less camber and less lift. Attempts to launch and fly the large *M. ater* in a 17-m flight chamber have proved unsuccessful (Altenbach, personal communication). Several molossid species need an elevated place to drop from to get enough lift to fly. Little quantitative and comparative flight data among molossid species have been collected, and what data that have are difficult to compare because of differing techniques from study to study. Struhsaker (1961) calculated a higher aspect ratio in *Tadarida brasiliensis* rather than in *Molossus nigricans* (=*M. ater*). This could mean that *T. brasiliensis* is the faster flier, if higher aspect ratio does indicate faster flight as Vaughan (1959, 1966) suggests; but *T. brasiliensis* flies easily in an enclosed room and can even take off from the floor. This species of *Tadarida* is also a smaller, lighter bat. The relative length of the last phalanx of digit IV is longer in *T. brasiliensis* (12.67 per cent) than in *M. ater* (4.84 per cent). Observations of where various species of *Molossus* fly support the fast flight idea. McNab (1971) mentioned that *M. molossus* flies above the canopy, and Fenton (1972) noted that *M. ater* and several other molossids were caught only in the upper levels of the canopy. Lawlor (1973, p. 76) reported that two species of *Molossus*, *M. ater*, and *M. bondae*, "fly only in areas of little obstruction, commonly above the tree canopy, as they feed upon insects," and D.C. Carter (personal communication) has netted *Molossus* either over deep pools or streams

TABLE 7. Nearest of most highly correlated neighbors of each bat from size-in distance, size-out distance, and the correlation matrices. At least two neighbors are given for each bat, but three are given for species of *Eumops* and species in the Conglomerate (*Molossops*, etc.). A small distance value or a large correlation value indicates a high degree of phenetic similarity between two bats.

Tadarida

Species	Distance size-in	Distance size-out	Correlation
T AEGYPA	E BONADA .608; TC ALOYA .618	T BRASIA .393; TR KALIN .459	T TENIOA .694; T BRASIA .645
T AFRICA	T FULMIN .681; T LOBATA .715	T FULMIN .453; T LOBATA .555	T FULMIN .775; T AUSTRA .630
T ANSORA	TC RUSSA .355; TC NIGEA .372	TC BIVIA .256; TC ALOYA .337	TC BIVIA .778; TC RUSSA .722
T AURISA	T FEMORA .528; T LATICA .615	T FEMORA .420; T LATICA .425	T FEMORA .882; T MACROA .785
T AUSTRA	T TENIOA .530; T KUBORI .637	T TENIOA .518; T BRASIA .588	T TENIOA .814; T KUBORI .687
T BRASIA	TR PLANA .560; TR KALIN .578	T AEGYPA .393; TR KALIN .468	T AEGYPA .645; TR KALIN .613
T FEMORA	T AURISA .528; T LATICA .557	T AURISA .420; T MACROA .508	T AURISA .883; T MACROA .780
T FULMIN	T LOBATA .436; T TENIOA .605	T LOBATA .432; T AFRICA .453	T LOBATA .809; T AFRICA .775
T KUBORI	T FULMIN .635; T AUSTRA .637	T BRASIA .578; T AUSTRA .602	T AUSTRA .687; T TENIOA .555
T LATICA	T FEMORA .557; T ANSORA .565	T AURISA .425; TC ALOYA .523	T AURISA .682; T FEMORA .598
T LOBATA	T FULMIN .436; T TENIOA .638	T FULMIN .432; T AFRICA .555	T FULMIN .809; T AFRICA .725
T MACROA	T AURISA .613; T TENIOA .650	T FEMORA .508; T AURISA .526	OTO MARA .799; T AURISA .785
T TENIOA	T AUSTRA .530; T FULMIN .605	T AUSTRA .518; T AEGYPA .521	T AUSTRA .814; T FULMIN .713

Cheerephon

Species	Distance size-in	Distance size-out	Correlation
TC ALOYA	TC BIVIA .366; T ANSORA .505	T ANSORA .337; TC RUSSA .357	TC RUSSA .660; T ANSORA .624
TC BEMMI	T ANSORA .438; TC MAJOR .467	TC BIVIA .381; TC MAJOR .450	TC BIVIA .620; TC CHAPI .591
TC BIVIA	TC ALOYA .366; T ANSORA .394	T ANSORA .256; TC NIGEA .348	T ANSORA .778; TC RUSSA .665
TC CHAPI	TM NANUA .587; TR PLANA .600	TC BIVIA .397; TC MAJOR .410	TC MAJOR .645; TC NIGEA .644
TC JOBEN	TM NIVEA .511; TM CONDA .516	TM TREVO .493; TC PLICA .510	TM CONDA .517; TM SABSA .503
TC JOHOR	TC BEMMI .505; TC MAJOR .513	TC CHAPI .440; TC MAJOR .468	TC BEMMI .569; TC CHAPI .549
TC MAJOR	TC PUMIA .412; T ANSORA .425	TC BIVIA .363; TC NIGEA .375	TC CHAPI .645; TC NIGEA .612
TC NIGEA	T ANSORA .372; TC RUSSA .401	TC BIVIA .348; T ANSORA .367	TC RUSSA .664; T ANSORA .652
TC PLICA	T ANSORA .419; TC BIVIA .482	TC BIVIA .406; TC PUMIA .411	TC PUMIA .593; T ANSORA .501
TC PUMIA	TC MAJOR .412; T ANSORA .445	TC BIVIA .355; T ANSORA .386	TC CHAPI .632; T ANSORA .581
TC RUSSA	T ANSORA .355; TC NIGEA .401	T ANSORA .355; TC ALOYA .357	T ANSORA .722; TC NIGEA .664

Table 7. *Continued.*

Mops

	Distance size-in		Distance size-out		Correlation	
TM BRACH	TM THERA .335	TM LEONA .557	TM THERA .335	TM TREVO .413	TM THERA .837	TM NANUA .735
TM CONDA	TC JOBEN .516	TM NIVEI .523	TM DEMOA .490	TM CONGA .492	TM DEMOA .570	TC JOBEN .517
TM CONGA	TM TREVO .526	TM NIANG .605	TM DEMOA .391	TM SARSA .445	TM MIDAA .690	TM TREVO .637
TM DEMOA	TM NIVEI .451	TM SARSA .522	TM NIVEI .351	TM MIDAA .362	TM NIVEI .710	TM SARSA .587
TM LEONA	TM THERA .516	TM BRACH .557	TM NANUA .394	XIPHONYC .402	XIPHONYC .841	TM NANUA .829
TM MIDAA	TM CONGA .615	TM TREVO .851	TM DEMOA .362	TM NIVEI .374	TM CONGA .690	TM TREVO .536
TM MOPSA	TM SARSA .407	TM DEMOA .550	TM SARSA .397	TM NANUA .480	TM SARSA .750	TM LEONA .521
TM NANUA	XIPHONYC .497	TM LEONA .585	TM LEONA .394	TM BRACH .445	TM LEONA .829	XIPHONYC .793
TM NIANG	TM TREVO .424	TM CONGA .605	TM TREVO .417	TM NIVEI .468	TM TREVO .691	TM CONGA .595
TM NIVEI	TM DEMOA .451	TC JOBEN .511	TM DEMOA .351	TM TREVO .378	TM DEMOA .710	TM TREVO .573
TM SARSA	TM MOPSA .407	TM DEMOA .522	TM MOPSA .397	TM CONGA .445	TM MOPSA .750	XIPHONYC .604
TM TREVO	TM NIANG .424	TM CONGA .526	TM THERA .374	TM NIVEI .378	TM NIANG .691	TM CONGA .637
TM THERA	TM BRACH .335	TM LEONA .516	TM BRACH .335	TM TREVO .374	TM BRACH .837	XIPHONYC .721
XIPHNYC	TM NANUA .497	TM LEONA .613	TM LEONA .402	TM NIVEI .472	TM LEONA .841	TM NANUA .793

Mormopterus - Sauromys - Platymops

	Distance size-in		Distance size-out		Correlation	
TR ACETA	TR KALIN .492	TR PHRUD .535	TR MINUA .467	TR KALIN .491	TR MINUA .712	TR KALIN .695
TR BECCR	TR JUGUA .658	TR NORFA .831	TR JUGUA .595	TR NORFA .618	TR JUGUA .701	TR NORFA .688
TR JUGUA	TR NORFA .557	TR PHRUD .571	TR NORFA .483	TR PHRUD .518	TR PHRUD .787	TR KALIN .764
TR KALIN	TR PHRUD .359	TR NORFA .439	TR PHRUD .336	TR MINUA .408	TR PHRUD .803	TR JUGUA .764
TR LORIA	TR NORFA .413	TR PLANA .480	TR NORFA .400	TR PLANA .471	TR NORFA .796	TR PLANA .724
TR MINUA	TR KALIN .504	TR PHRUD .514	TR PHRUD .292	TR KALIN .408	TR NORFA .780	TR PLANA .775
TR NORFA	TR PLANA .296	TR LORIA .413	TR PLANA .295	TR LORIA .400	TR PLANA .880	TR LORIA .796
TR PHRUD	TR KALIN .359	TR NORFA .435	TR MINUA .292	TR KALIN .336	TR KALIN .803	TR JUGUL .787
TR PLANA	TR NORFA .296	TR KALIN .460	TR NORFA .295	TR MINUA .435	TR NORFA .880	TR MINUA .775
SAUROMYS	TR NORFA .570	TR PLANA .597	TR NORFA .448	TR PLANA .475	TR NORFA .663	TR KALIN .661
PLATYMOP	SAUROMYS .724	TR PLANA .750	TR ACETA .673	TR MINUA .682	TR ACETA .622	TR MINUA .602

TABLE 7. Continued.

Moloscops - Neoplatymops - Cynomops - Myopterus - Cheiromeles

Left group

	Distance size-in		Distance size-out		Correlation	
MP TEMMA	NEOPLATA	.492	NEOPLATA	.491	NEOPLATA	.744
	TR LORIA	.575	CP PLANA	.518	TR LORIA	.652
	CP PLANA	.587	TR MINUA	.563	CP PLANA	.644
NEOPLATA	MP TEMMA	.492	MP TEMMA	.491	MP TEMMA	.744
	TR MINUA	.560	TR MINUA	.534	TR MINUA	.624
	TR LORIA	.611	E UNDERA	.550	PLATYMOP	.586
CP BRACA	TM MIVEI	.727	CP PLANA	.303	CP GREEA	.693
	PRO CEM	.784	CP GREEA	.382	C PARVID	.635
	M ATERA	.788	MP TEMMA	.594	CP PLANA	.599
CP GREEA	CP PLANA	.410	CP PLANA	.306	CP PLANA	.797
	MYOP WHA	.615	CP BRACA	.381	CP BRACA	.693
	TC MAJOR	.623	TR MINUA	.592	M BONDAA	.451
CP PLANA	CP GREEA	.410	CP BRACA	.303	CP GREEA	.797
	MP TEMMA	.587	CP GREEA	.306	MP TEMMA	.644
	MYOP WHA	.629	MP TEMMA	.518	CP BRACA	.599
MYOP ALB	TM NIANG	.757	MYOP WHA	.528	C PARVID	.501
	M ATERA	.817	MP TEMMA	.666	MYOP WHA	.474
	TM TREVO	.845	NEOPLATA	.700	CP BRACA	.465
MYOP WHA	CP GREEA	.615	MYOP ALB	.528	MP TEMMA	.566
	CP PLANA	.629	MP TEMMA	.578	M COIBEA	.491
	M COIBEA	.721	TR MINUA	.595	M BONDAA	.479
C PARVID	C TORQUT	.301	C TORQUT	.278	C TORQUT	.982
	E UNDERA	1.510	MP TEMMA	.862	CP BRACA	.635
	E PEROTA	1.882	TR LORIA	.899	E UNDERA	.597
C TORQUT	C PARVID	.301	C PARVID	.278	C PARVID	.982
	E UNDERA	1.493	MP TEMMA	.907	CP BRACA	.627
	E PEROTA	1.888	TR JUGUA	.943	E UNDERA	.547

Eumops

	Distance size-in		Distance size-out		Correlation	
E AURIPA	E GLAUCA	.584	M BONDAA	.523	E GLAUCA	.714
	TM NIANG	.658	M SINALA	.566	E UNDERA	.597
	TM CONGA	.660	E GLAUCA	.578	M ATERA	.596
E BONARA	TC NIGEA	.548	E UNDERA	.476	E PEROTA	.542
	TC BIVIA	.578	TR MINUA	.529	T LOBATA	.481
	TC ALOYA	.585	TR PLANA	.585	T AFRICA	.448
E GLAUCA	E AURIPA	.584	E MAURUS	.499	E UNDERA	.736
	T AFRICA	.760	E UNDERA	.566	E AURIPA	.714
	E MAURUS	.790	E AURIPA	.578	E MAURUS	.663
E HANSAA	E BONARA	.743	E BONARA	.690	T AURISA	.353
	TC MAJOR	.755	T AURISA	.739	E BONARA	.302
	T AURISA	.805	TC MAJOR	.750	T FEMORA	.302
E MAURUS	E BONARA	.662	E GLAUCA	.499	E GLAUCA	.663
	TC ALOYA	.669	E UNDERA	.605	E AURIPA	.547
	TC BIVIA	.672	E BONARA	.620	E UNDERA	.443
E PEROTA	E UNDERA	.800	E BONARA	.702	E UNDERA	.795
	T AFRICA	1.195	T LOBATA	.737	OTO MARA	.706
	TM MIDAA	1.225	T FEMORA	.753	T AFRICA	.681
E UNDERA	E PEROTA	.800	E BONARA	.476	E PEROTA	.795
	TM MIDAA	.889	TR MINUA	.538	E GLAUCA	.736
	T AFRICA	.982	NEOPLATA	.550	T AFRICA	.674

48

Table 7. *Continued.*

Molossus

	Distance size-in		Distance size-out		Correlation	
M ATERA	M PRETIA .536	M SINALA .619	M SINALA .312	M BONDAA .317	M SINALA .851	M PRETIA .813
M BONDAA	M MOLOSS .360	M SINALA .406	M COIBEA .251	M ATERA .317	M COIBEA .919	M MOLOSS .900
M COIBEA	M MOLOSS .439	M BONDAA .446	M BONDAA .251	M MOLOSS .375	M BONDA .919	M MOLOSS .871
M MOLOSS	M BONDAA .360	M COIBEA .439	M SINALA .293	M BONDAA .332	M BONDAA .900	M SINALA .895
M PRETIA	M ATERA .536	M SINALA .607	M ATERA .477	M SINALA .532	M ATERA .813	M SINALA .765
M SINALA	M BONDAA .406	M MOLOSS .450	M MOLOSS .293	M ATERA .312	M MOLOSS .895	M BONDAA .856
M TRINIT	M BONDAA .425	M SINALA .465	M BONDAA .423	M SINALA .434	M SINALA .802	M BONDAA .792

Otomops - Promops - Vespertilionids

	Distance size-in		Distance size-out		Correlation	
OTO MARA	OTO WROA .574	T TENIOA .775	OTO WROA .412	OTO SECA .557	OTO WROA .928	T MACROA .799
OTO PAPU	OTO SECA .513	TC PLICA .729	OTO SECA .497	OTO WROA .555	OTO SECA .819	OTO WROA .704
OTO SECA	OTO PAPU .513	OTO WROA .742	OTO WROA .327	OTO PAPU .497	OTO WROA .903	TO PAPU .819
OTO WROA	OTO MARA .574	T TENIOA .680	OTO SECA .327	OTO MARA .412	OTO MARA .928	OTO SECA .903
PRO CENA	PRO NASU .559	M SINALA .646	PRO NASU .313	M TRINIT .510	PRO NASU .818	M SINALA .540
PRO NASU	PRO CENA .559	M TRINIT .596	PRO CENA .313	M TRINIT .595	PRO CENA .818	M SINALA .573
MIMETILL	TR PHRUD .858		NYCTALUS .765		TR PHRUD .597	
NYCTALUS	T AEGYPA .833		MIMETILL .765		MIMETILL .534	

49

TABLE 8. Average least distance (size-out) among taxa. The method for calculating these averages is explained in the text and in Figure 8. The treatment of the four genera below the line is explained in the Evolutionary Relationships section.

	Tadarida	Chaerephon	Mops	Mormopterus	Cheiromeles	Cynomops	Eumops	Molossops	Molossus	Myopterus	Neoplatymops	Otomops	Platymops	Promops	Sauromys	Vespertilionidae	Tadarida	Nyctinomops	Mormopterus	Molossops
Tadarida	0.0																			
Chaerephon	0.743	0.0																		
Mops	0.983	0.673	0.0																	
Mormopterus	0.799	0.746	0.828	0.0																
Cheiromeles	1.441	1.252	1.178	1.023	0.0															
Cynomops	1.003	0.815	0.756	0.761	0.974	0.0														
Eumops	0.846	0.784	0.874	0.829	1.404	0.859	0.0													
Molossops	1.029	0.787	0.744	0.706	0.884	0.579	0.895	0.0												
Molossus	1.145	0.907	0.792	0.955	1.250	0.786	0.893	0.837	0.0											
Myopterus	1.088	0.872	0.782	0.788	1.078	0.720	0.895	0.618	0.794	0.0										
Neoplatymops	0.952	0.775	0.718	0.681	1.024	0.640	0.782	0.491	0.876	0.668	0.0									
Otomops	0.829	0.910	1.152	1.100	1.743	1.278	1.024	1.262	1.331	1.270	1.128	0.0								
Platymops	1.032	0.928	0.937	0.752	1.112	0.879	0.960	0.737	1.018	0.798	0.700	1.290	0.0							
Promops	0.943	0.786	0.861	0.852	1.260	0.775	0.818	0.704	0.687	0.794	0.820	1.131	1.000	0.0						
Sauromys	0.711	0.751	0.890	0.570	1.154	0.879	0.829	0.829	1.005	0.844	0.754	1.046	0.711	0.862	0.0					
Vespertilionidae	1.086	1.148	1.123	0.896	1.237	1.082	1.195	1.070	1.199	1.116	0.912	1.303	1.020	1.216	0.852	0.0				
Tadarida (Old World, T BRASIA)	0.0	0.741	0.985	0.760	1.396	0.974	0.855	0.992	1.156	1.052	0.930	0.851	0.963	0.934	0.676	1.030	0.0			
Nyctinomops	0.0	0.747	0.979	0.878	1.530	1.060	0.828	1.104	1.122	1.160	0.995	0.785	1.170	0.961	0.780	1.197	0.723	0.0		
Mormopterus (Platymops, Sauromys)	0.0	0.763	0.843	0.0	1.043	0.838	0.861	0.965	0.794	0.689	1.112	0.815	0.0	0.866	0.770	0.996	0.771	0.895	0.0	
Molossops (Cynomops, Neoplatymops)	0.0	0.801	0.746	0.742	0.966	0.0	0.851	0.0	0.775	0.689	0.0	1.245	0.815	0.770	0.844	1.046	0.969	1.056	0.785	0.0

TABLE 9. Moth scale counts from fecal samples of various molossid species (method modified after Black, 1974).

Species	Scales/gram	Remarks	Species	Scales/gram	Remarks
Molossus ater	0		Molossus sinaloae	1,257	
Molossus ater	842	Non-moth leg	Molossus sinaloae	1,359	Beetle parts, seeds?
Molossus ater	870		Molossus sinaloae	1,360	
Molossus ater	2,250	Beetle parts (legs, antennae, or mouth parts)	Molossus sinaloae	4,188	Beetle parts?, Lepidopteran
Molossus bondae	222		Molossops greenhalli	0	Beetle parts?
Molossus bondae	762				
Molossus coibensis	0	Beetle parts	Tadarida brasiliensis	1,702	
Molossus coibensis	0	Beetle exoskeleton	Tadarida brasiliensis	1,823	
Molossus coibensis	0	Beetle mandible	Tadarida brasiliensis	2,452	
Molossus coibensis	0		Tadarida brasiliensis	3,196	Non-moth, Dipteran parts
Molossus coibensis	0		Tadarida brasiliensis	119,596	Moth parts, Dipteran?
Molossus coibensis	0				
Molossus coibensis	119	Beetle part, Hymenopteran?	Tadarida macrotis	16,726	
Molossus coibensis	1,231	Dipteran?, Hymenopteran?	Tadarida macrotis	33,929	Moth parts
Molossus coibensis	1,515		Tadarida macrotis	138,648	
Molossus coibensis	1,525		Tadarida macrotis	144,032	Moth parts
Molossus coibensis	1,818				
Molossus coibensis	2,045				
Molossus coibensis	2,525				
Molossus coibensis	17,973				
Molossus coibensis	23,333				
Molossus pretiosus	0	Beetle parts			
Molossus pretiosus	62	Beetle parts			
Molossus pretiosus	260	Beetle parts			
Molossus pretiosus	2,203				
Molossus sinaloae	75	Beetle parts, seeds?			
Molossus sinaloae	897				

or on forest roads and paths. No species of *Molossus* seem to roost in caves; rather, they are found in small colonies under palm leaves, in hollow trees, under roofs, in sheds and attics, in crevices of cliffs, and under bridges.

Promops

Promops consists of two Neotropical species, *P. centralis* and *P. nasutus*, which are difficult to distinguish from some species of *Eumops* on the PCA (fig. 4). *Promops* is very *Molossus*-like, but is slightly less robust in jaw proportions (mean relative dentary thickness is 12 per cent, see table 6) and in development of sagittal and lambdoidal crests. Like *Molossus*, *Promops* has ears neither joined by a band over the nose nor completely separated, moderately deep basi-sphenoid pits, lips without wrinkles, narrow-tipped wings, and V-shaped M³'s. Unlike *Molossus*, *Promops* bears a vestigial PM³ (fig. 10).

Nearest neighbor distances and correlation place the two species of *Promops* closest to one another, but the next nearest neighbors are members of *Molossus*, particularly *M. trinitatus* (size-out distance, table 7). The latter is a species of *Molossus* of slightly less robust build than other species of the genus, and its similarity to *Promops* is substantiated by its positioning on the PCA plots (fig. 4). Besides *Molossus*, *Promops* has near neighbors among species of *Eumops*, particularly *E. glaucinus*, *E. maurus*, and *E. underwoodi*. These neighbors are closer than *Molossops* or species of *Cynomops*.

The intrageneric distance, size-out, is 0.313, a compact average third only to that of *Cheiromeles* and *Cynomops* (table 5). The size-in average is large, 0.559, a reflection of the size difference between the two species.

Among genera, *Promops* averages 0.687 in size-out distance from *Molossus*, 0.704 from *Molossops*, and 0.775 from *Cynomops* (table 8). It is farthest from *Cheiromeles* at 1.260.

The larger *Promops centralis* (GSL = 20.0 mm) is about the size of *Molossus pretiosus*, and the smaller *Promops nasutus* (GSL = 17.7 mm) is about the size of *M. molossus* or *M. bondae*. Like *Molossus*, both species of *Promops* are very similar in shape to each other.

Ecologically, species of *Promops* are probably like those in *Molossus* in that they have the same narrow-tipped wings, but they may take foods that are not as hard because they have slightly less robust jaws and skulls. Food and flight data are nonexistent. Species of *Promops* have been found under bark in the tops of trees (Brosset, 1966), obtained from hollow trees (Jones, 1966), and captured over a shallow pond surrounded by pine-oak forest (LaVal, 1969).

Mops

Species of *Mops* lie to the lower left of *Molossus* on the PCA plots (fig. 4). OTU's included in the cluster of *Mops* are: *M. brachyptera*, *M. condylura*, *M. congica*, *M. demonstrator*, *M. leonis*, *M. midas*, *M. mops*, *M. nanula*, *M. niangarae*, *M. niveiventer*, *M. sarasinorum*, *M. trevori*, *M. thersites*, *Xiphonycteris spurrelli*, and one species of *Chaerephon*, *C. jobensis*. These bats are found mostly in Africa, but a few species occur in the Indo-Australian region. *Mops* is presently regarded as a subgenus of *Tadarida*, but in my study they form a distinct group fairly distant from *Tadarida*. *Xiphonycteris spurrelli* has been considered a genus (Rosevear, 1965; Hayman & Hill, 1971), but here it clusters with species of *Mops*.

As suggested by the placement on axis II and also axis III, dentaries of species of *Mops* are slightly less robust than those in *Molossus* (mean relative dentary
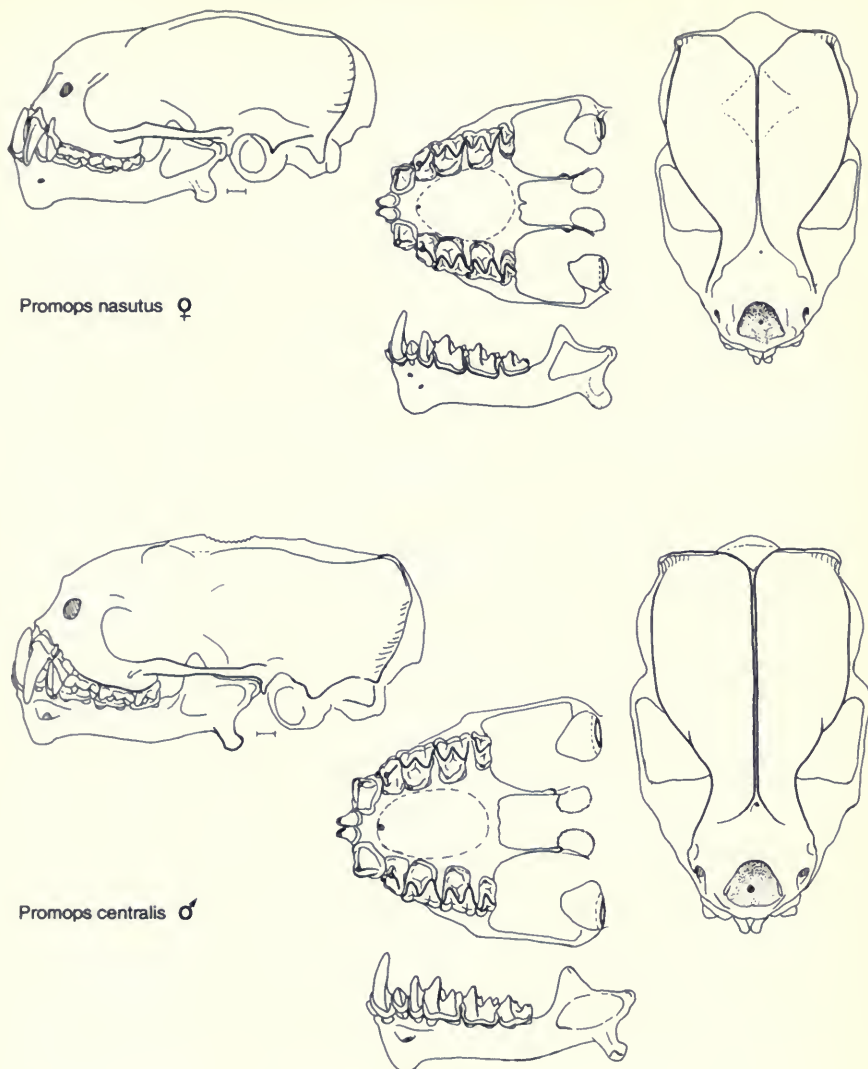
FIG. 10. Two species of *Promops*. Lateral, dorsal, and palatal views of the skull and lateral view of the mandible are given for both.

thickness is 13.2 per cent) as are other jaw proportions except height of the mandibular condyle above the toothrow (table 6). Species of *Mops* do not have the extreme sagittal crest development of that in *Molossus* nor is the posterior commissure on the third upper molar completely lost (except in *Mops mops* and *M. sarasinorum*, both Indo-Australian species). The third upper premolar shows variable states, from absent in *M. mops* to poorly developed in most of the African forms, and large in *Xiphonycteris* (fig. 11). Ears of species of *Mops* are joined over the nose with a band, basisphenoid pits vary from shallow to deep, and the lips are very wrinkled (appendix A).

Mops spurrelli ♂
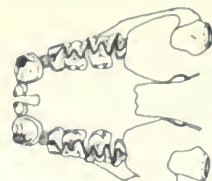
Mops nanula ♂
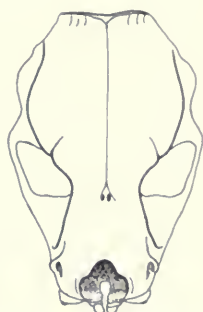
Mops leonis ♀
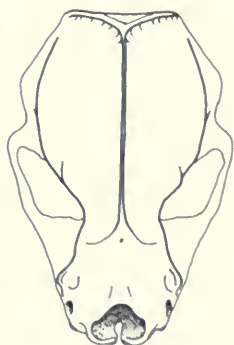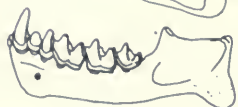
Mops brachyptera ♀

FIGURE 11.

54
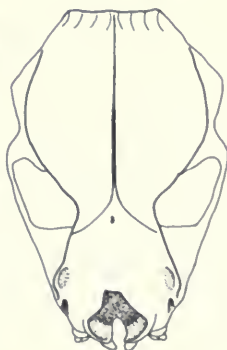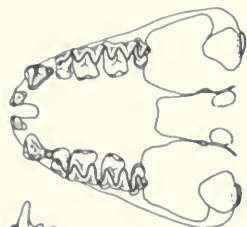
Mops thersites ♂
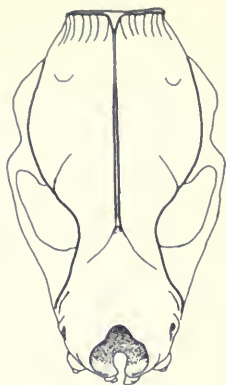
Mops sarasinorum ♂

Mops demonstrator ♂

FIGURE 11.

55
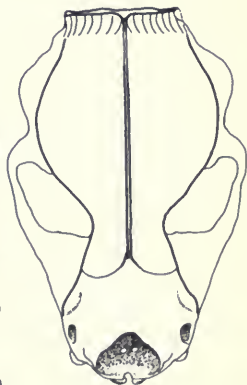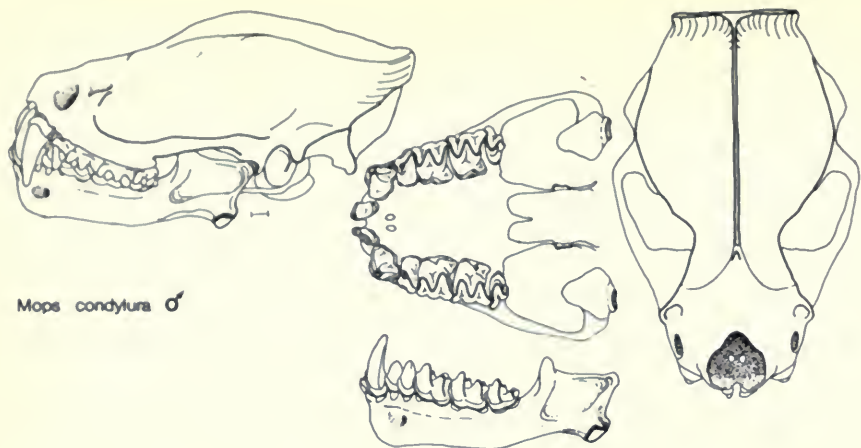
Mops condylura ♂
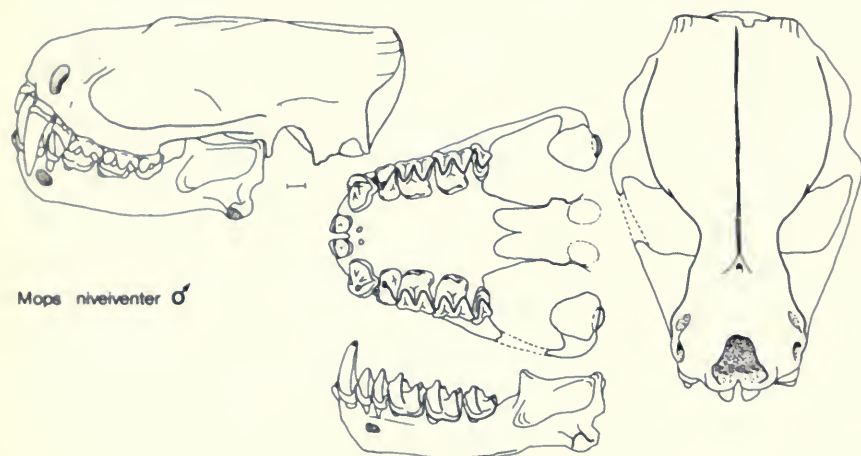
Mops niveiventer ♂

Mops mops ♂

FIGURE 11.

56

Mops niangarae ♂

Mops congica ♂

FIGURE 11.

57

Mops midas ♂
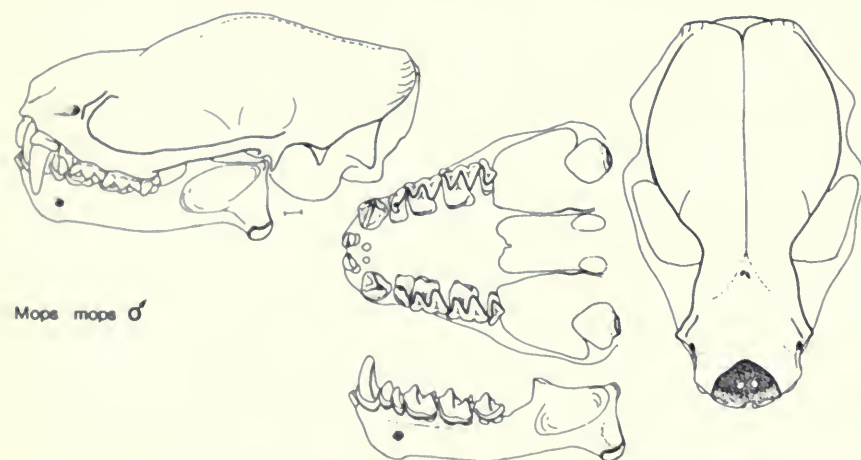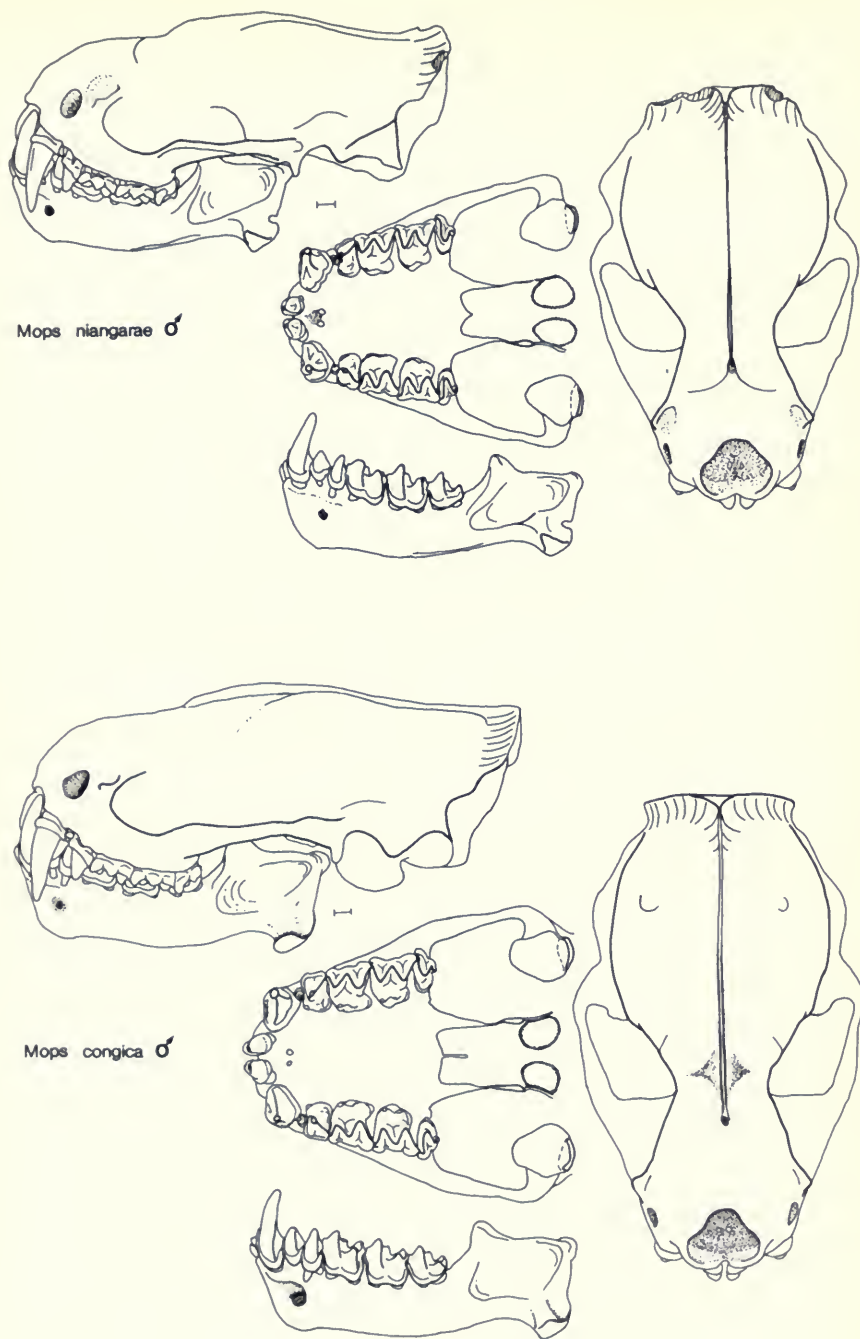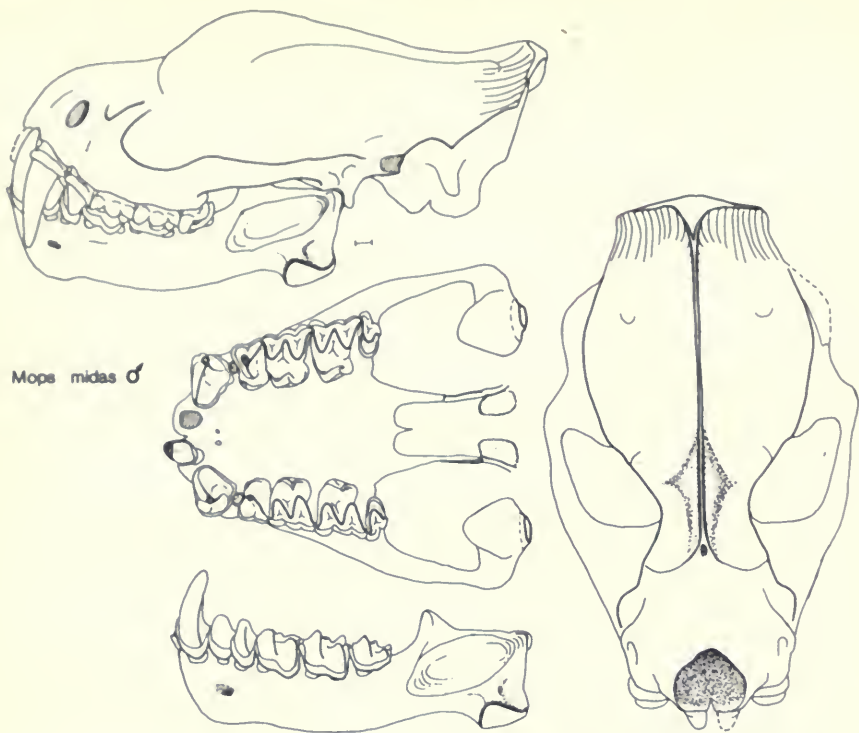
FIG. 11. Thirteen species of *Mops* arranged from small to large. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible are given for all 13.

Characters that distinguish species of *Mops* from species of *Molossus* on axis IV are broad wing tips (mean of relative length of second phalanx of digit IV is 16.2 per cent), little development of the lateral lambdoidal crest (although great development of superior lambdoidal), many wrinkles, and large ears. The two clusters, *Mops* and *Molossus*, are opposites on this axis.

Species of *Mops* are distinctly separate from species of Old World *Tadarida* and *Chaerephon* because of the relatively shorter M^3 (posterior ridge reduced) and better developed sagittal and lambdoidal crests. Although there is some morphological overlap with *Tadarida* and more with *Chaerephon*, species of *Mops* on the average have thicker dentaries, higher coronoid processes, more elevated condyles, and greater moment arm indices of the jaw muscles (table 6).

Xiphonycteris and *Chaerephon jobensis* are included in the cluster of species of *Mops* on the PCA. These two bats have characteristics similar to those of *Mops*, namely, thick jaws and many of the related jaw proportions and codes (table 6, appendix A). Even when the qualitative multistate characters (codes) are removed from the PCA, these two species cluster with species of *Mops*.

Clustering techniques confirm the impression given by the PCA. With one exception all nearest neighbors in distance (size-in and size-out) are members of *Mops* and all highest positively correlated neighbors are species of *Mops* as

well (table 7). *Xiphonycteris* is closest either to *Mops nanula* or *M. leonis*, all three of which are members of what Koopman (1975) referred to as *Tadarida* (*Xiphonycteris*). In the size-in analysis, the nearest neighbor of *Mops condylura* is *Chaerephon jobensis*. The closest neighbors of *C. jobensis* in the clustering methods are species of *Mops* (table 7).

Average least distance within the taxa both with size excluded and size included is relatively low (table 5). Size-out average of 0.385 is below the dividing point between compact and dispersed groups, and the size-in average is 0.458, also below the average in the size-in matrix. (These figures include *Xiphonycteris* but not *Chaerephon jobensis*.) Average least distance (size-out) among genera in Table 8 shows *Chaerephon* the closest (0.673) to *Mops* and *Cheiromeles* and *Otomops* the farthest (1.178 and 1.152) from *Mops*.

Though individual codes of shape are not as uniform for *Mops* as for *Molossus*, the species look much alike but are of different sizes (fig. 11). The range of sizes in this group is greater than in *Molossus* and, indeed, greater than in any other genus in the study (from 14.9 mm GSL in *Xiphonycteris* and 15.0 mm in *Mops nanula* to 27.0 mm in *M. midas*, see table 1).

I judge the functional capabilities of the jaws in *Mops* to be much like those of *Molossus*, though the jaws and skull are slightly less robust in build. The average relative height of condyle above the toothrow for *Mops* is greater than that in *Molossus* and may give some greater mechanical advantage to make up for a slightly less robust skull. Wings in species of *Mops* are among the broadest-tipped of any of the taxa. The camber produced by the long second phalanx is probably considerable and allows for more maneuverability and possibly slower flight than in *Molossus*. Perhaps species of *Mops* are capable of eating hard-bodied prey as do *Molossus*, but species of *Mops* may not fly like species of *Molossus*. Although little evidence is available for the first contention, Verschuren (1957) reported that stomachs of *Mops condylura* contained legs of *Coleoptera*. Lang & Chapin (1917, p. 491) noted that, "The heavy skull of *Mops* (*Allomops*) *osborni* [= *M. condylura*] (Fig. 12, pg. 470), with an enormous sagittal and lambdoid crest, is capable of giving strong support to large muscles of mastication. They are needed to operate the broad grinding, cutting surfaces of the short dental rows. The food of all such Molossidae consists chiefly of hard-shelled insects." Recently, Whitaker & Mumford (1978) reported that nine *Tadarida condylura* (= *Mops condylura*) had consumed 65 per cent Coleoptera, 20.6 per cent Hemiptera, and 11.7 per cent Lepidoptera. Anecdotally, Randolph Peterson told me that *condylura* had a particularly strong bite.

Support for the contention that *Mops* is slower and more maneuverable in flight than *Molossus* is not extensive. Several authors call *midas, trevori, condylura,* and *demonstrator* savannah species and *congica, niangarae, thersites, leonis* and *nanula* and *Xiphonycteris* forest species (Lang & Chapin, 1917; Verschuren, 1957; Rosevear, 1965; Hayman & Hill, 1971). *Mops condylura,* like many species of *Molossus,* has been found in houses and its widespread distribution includes forest and savannah habitats (Rosevear, 1965). Peterson (1972) stated that the larger species of *Mops* did not seem to overlap ecologically and that *congica* is in high forest (following Rosevear's ecological description), *trevori* is at forest edge or in open forest, and *midas* is in savannah or isolated savannah forests. In conclusion, most species of *Mops* seem to live in places with obstacles in them; few are found in strictly open areas.

Chaerephon

A third compact group to the left of *Mops* on the negative side of the jaw axis is mainly comprised of species of *Chaerephon*, a classical subgenus of *Tadarida*, and like *Mops*, mostly African with a few species found in the Indo-Australian region (figs. 4, 12). The species included here are *C. aloysiisabaudiae*, *C. bivittata*, *C. chapini*, *C. bemmelini*, *C. johorensis*, *C. major*, *C. nigeriae*, *C. plicata*, *C. pumila*, *C. russata*, and a species of *Tadarida*, *T. ansorgei*. Corresponding to the placement of the group on axis II, species of *Chaerephon* have a less robust jaw structure and thinner dentaries (mean of relative dentary thickness is 11.0 per cent). Like *Mops*, however, *Chaerephon* has a similar configuration of ears joined by a band over the nose and the same broad-tipped wings (mean of relative length of second phalanx is 16 per cent). *Chaerephon* has less development of sagittal and lambdoidal crests than *Mops*. Height of condyle above the toothrow is less than that in *Mops* but similar to that in *Molossus*. The posterior commissure on M^3 is at least moderately developed in all species except *pumila*. *Chaerephon jobensis* is exceptional for a species of *Chaerephon* in that its sagittal and lambdoidal crests are well developed and its dentary is thick (14 per cent of dentary length). As mentioned in the *Mops* account, this Indo-Australian *Chaerephon* seems to have more similarities with *Mops* than with *Chaerephon*. The important features which distinguish *Chaerephon* from *Mops* and *Tadarida* are listed in Table 6. *Chaerephon* is distinct from the latter by having a more constricted anterior palatal emargination, well-joined ears, broader wing tips, and on the average a more elevated mandibular condyle and greater moment arm index. *Chaerephon* overlaps with *Tadarida* in relative length of M^3 (though this N-shape is less developed in *Chaerephon*), relative dentary thickness, and relative height of coronoid process, and overlaps with *Mops* in wing tip width and several jaw characters.

A species now in *Tadarida*, *T. ansorgei*, is like *Chaerephon* in many jaw characteristics and in coded characteristics (table 5 and appendix A). Although Koopman (1975) placed *ansorgei* along with *Chaerephon bemmelini* and *Chaerephon bivittata* into the subgenus *Tadarida*, I cannot agree with this consignment because of the evidence from the PCA and the clustering techniques which suggest that these three species are members of *Chaerephon*. *Tadarida ansorgei*'s nearest neighbor, size-in, is *Chaerephon nigeriae* at 0.358 (low for size-in) and for size-out is *Chaerephon bivittata* at 0.277. This last distance is so low that one wonders if the two bats may not be members of the same species. The bat with the highest positive correlation with *ansorgei* is also *bivittata*. The three questionable species (*T. ansorgei*, *C. bemmelini*, and *C. bivittata*) are close to other members of *Chaerephon* and not to *Tadarida* (table 7). If one considers *T. ansorgei* a species of *Chaerephon*, then nearly all members of the genus have congeners as nearest neighbors in the three clustering methods. The exception is *jobensis* which is closest to a species of *Mops* in all these analyses. *Chaerephon chapini*, a small bat, is nearest *Mops nanula*, another small bat, in the size-in distance analysis.

Within-taxon average distance (size-out) for *Chaerephon* is on the compact side (0.364, *ansorgei* and *jobensis* included). Nearest neighbors to *Chaerephon* among taxa are, as expected from placement on the PCA, *Mops* at 0.673, *Tadarida* at 0.743, *Mormopterus* at 0.746; and its farthest neighbor is *Cheiromeles* at 1.252 (tables 5, 8).

Body sizes of species of *Chaerephon* are medium and range from a GSL of 16.0 mm in *chapini* to 21.0 mm in *aloysiisabaudiae* and *jobensis.*

Not only do the species of *Chaerephon* have generally less robust jaws and skulls than species of *Mops,* they also have a condyle less elevated above the toothrow (mean relative condylar height is 12.9 per cent versus 14.8 per cent in *Mops*). Degrees of difference in this character are thought to be related to the effectiveness of the bite, but the advantages to the bat are not yet determined. Average dentary thickness for *Chaerephon* is even less if *jobensis* is excluded as a species (reduced mean relative thickness is 9.5 per cent) as are the characteristics moment arm index and relative coronoid height.

Because the species of *Chaerephon* have broad-tipped wings, they are probably slower, more maneuverable flyers among molossids. *Chaerephon* should be less capable than *Mops* of consuming hard prey items because of its thinner dentaries and generally less robust skull.

Few data are at hand about food habits. Allen (1939) mentioned a specimen of *Chaerephon limbatus* (=*C. pumila*) that was found to have eaten adult moths of the cotton bollworm, whereas Verschuren (1957) reported stomachs of *ansorgei* to contain wings of Formicidae, hymenopteran antennae, and coleopteran legs. Whitaker & Mumford (1978) reported that nine specimens of *pumila* had consumed 48.3 per cent Hemiptera, 18.4 per cent Coleoptera, 13.3 per cent Lepidoptera, 10.4 per cent Diptera and unidentified insects, and 8.3 per cent Orthoptera.

Recently, Vestjens & Hall (1977) reported on stomach contents in nine specimens of *Tadarida jobensis.* Eight of the nine had moth remains and three had remains of plant bugs and ants. There also was one occurrence each of ground beetles, water beetles, leaf beetles, unidentified beetles, flies, crickets, and earwigs. I think *jobensis,* with its thick jaws, can probably take anything up to the hardness of beetles.

Support is also weak for the postulated slower, more maneuverable flight of species of *Chaerephon.* Several, such as *russata, aloysiisabaudiae, bemmelini, pumila,* and *nigeriae,* have been found at forest edge or in forest situations (Peterson, 1971b; Fenton & Peterson, 1972; Verschuren, 1957; Rosevear, 1965). Others, however, such as *major, ansorgei,* and *chapini,* are considered savannah species (Lang & Chapin, 1917; Verschuren, 1957). *Chaerephon pumila* has been found in both places. Brosset (1966) reported that *plicata* has been found in immense groups in grottos in southern Asia.

Fenton (1972) divided several African molossids into two groups based on his metacarpal III/metacarpal V ratio. Four species of *Chaerephon* had a higher ratio than four species of *Mops* and were thought to be swifter. His measure did not take into account the phalanges. Based on the analysis in my study, both *Mops* and *Chaerephon* have very similar wing configurations, and I believe that they fly in the same way.

Otomops-Tadarida macrotis

The extreme cluster, opposite *Molossus,* on axis II consists of four bats: three species of *Otomops* (*O. papuensis* excluded) and *Tadarida macrotis* (fig. 4). This phenetically cohesive group occurs over a tremendous geographic area: *O. secundus* occurs in New Guinea, *O. wroughtoni* in India, *O. martiensseni* in Africa; and *T. macrotis* inhabits southwestern United States and much of Central and

Chaerephon chapini ♂
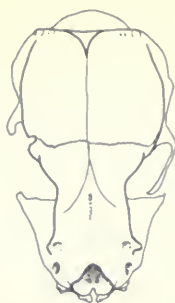
Chaerephon major ♀
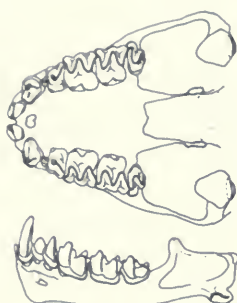
Chaerephon pumila ♂
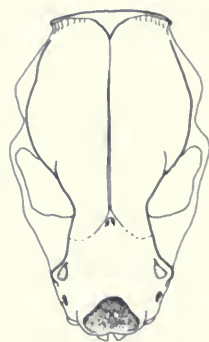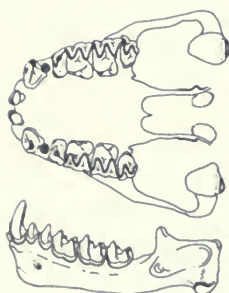
Chaerephon bemmelini ♂
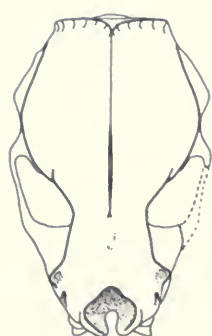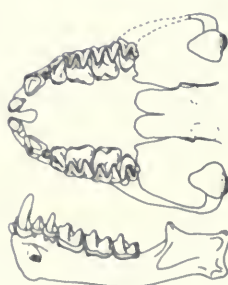
FIGURE 12.

62

Chaerephon nigeriae ♂
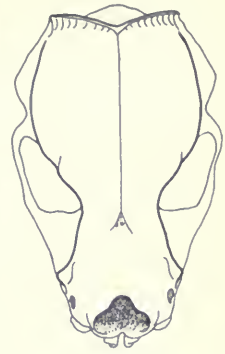
Chaerephon ansorgei ♂
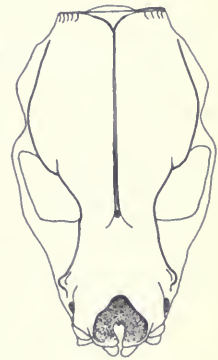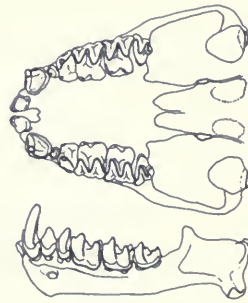
Chaerephon russata ♂

FIGURE 12.

63
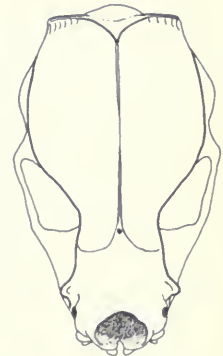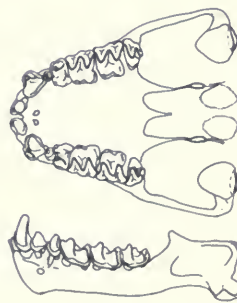
Chaerephon plicata ♂
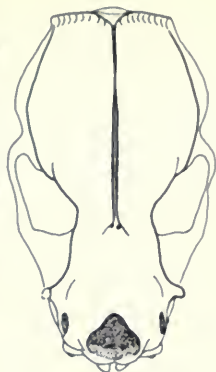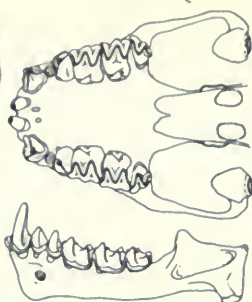
Chaerephon bivittata ♂
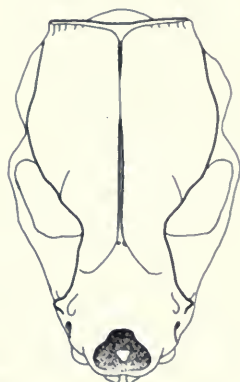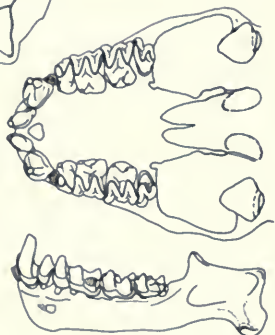
Chaerephon aloysiisabaudiae ♂

FIGURE 12.

64

Chaerephon jobensis ♂
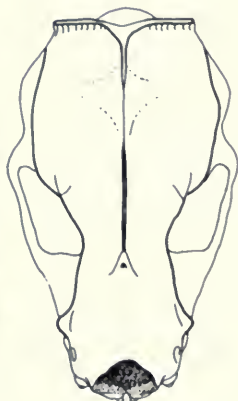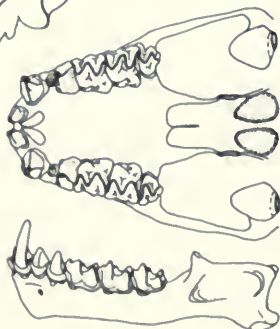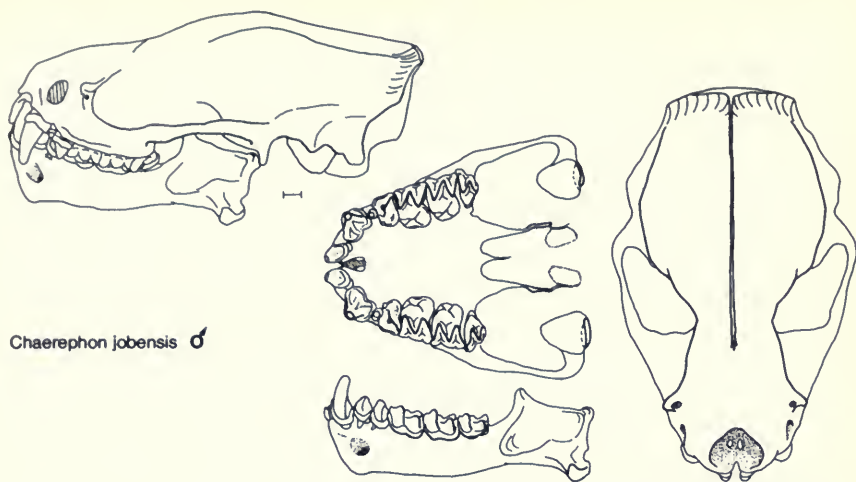
Fig. 12. Eleven species of *Chaerephon* arranged from small to large. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible are given for all 11.

South America. Characteristic of these bats are their very thin dentaries (mean relative dentary thickness is 9.0 per cent), low coronoid processes, presence of a large premolar well spaced between canine and PM⁴, M³ with full-sized posterior commissure (N-shaped), condyle not so elevated above the toothrow (mean relative condylar height is 6.0 per cent), and only slight development of sagittal and lambdoidal crests. The large ears are joined anteriorly over the nose, basisphenoid pits are very deep, and lips are wrinkled either finely or as deep troughs (table 6, appendix A).

Perhaps the small *Otomops papuensis*, *Eumops perotis*, and *Tadarida teniotis*, OTU's on the periphery of this cluster, should be included (fig. 4), but they do not have all of the extreme characteristics that occur in the *Otomops-T. macrotis* cluster. *Otomops papuensis* has a thicker dentary, and *E. perotis* has an almost V-shaped M³. *Tadarida teniotis* is not as extreme in the joining of the ears, development of the sagittal crest, or depth of the basisphenoid pits.

Only two variables are highly correlated with axis IV, and neither the species of *Otomops* nor *T. macrotis* are extreme in both of them. Although *T. macrotis* has extremely narrow wing tips (relative length of second phalanx is 3.1 per cent), it· has only a moderately developed lateral lambdoidal crest, and *Otomops* has only an intermediate wing tip (12.6 per cent) and no development of the crest.

To this point the PCA representation of the bats has corresponded for the most part with the clustering analyses. Although *Otomops* and *T. macrotis* are phenetically similar, the clustering analyses give a slightly different picture. In all three (size-in, size-out, and correlation), species of *Otomops* are closest to each other, including *O. papuensis* and excluding *T. macrotis*. The latter on the other hand is nearest other New World *Tadarida* in the two distance analyses but is most highly correlated with *O. martiensseni*.

Because of the nearest neighbors indicated by the clustering techniques, the summary averages, both within and among, follow generic groupings, placing all species of *Otomops* together and all species of *Tadarida* together. *Otomops'*

within-genus average (size-out), is 0.390, still within the range that I consider compact. The size-in average is 0.535, a number affected by the substantial variation in size among species of *Otomops*. Among genera, the nearest neighbor to *Otomops* is *Tadarida* (0.829) and the farthest neighbor is *Cheiromeles* (1.743). *Otomops* and *Cheiromeles* are the farthest apart of any two groups (tables 5, 8).

Greatest skull lengths of the similarly shaped species of *Otomops* and *Tadarida macrotis* are on the large side, at 19.7 mm and 27.2 mm in *O. papuensis* and in *O. martiensseni*, respectively, and at 23.0 mm in *T. macrotis* (table 1, figs. 5, 13).

The slender jaws of these bats are probably capable of a very wide gape because their coronoid processes are low and their mandibular condyle is almost in the same plane as the toothrow. Because of their jaw structure as well as the slight crest development, I think these bats are less capable of chewing up hard-shelled insects. The bats described in this section probably eat soft-bodied creatures such as moths, perhaps large ones. There is evidence, at least for the New World *T. macrotis*, that not only is there a large quantity of moth material in its feces (table 9), but that it is taking Macrolepidoptera, probably of the family Sphingidae (Ross, 1967). Easterla & Whitaker (1972) reported that in 98.0 per cent of 49 stomachs of *T. macrotis*, large moths made up 86.1 per cent of the volume. In 28.6 per cent of the stomachs, Gryllidae/Tettigoniidae made up 6.7 per cent of the volume, and in 8.2 per cent of the stomachs, Formicidae made up 4.1 per cent of the volume.

There is also qualitative evidence that the narrow wing-tipped *T. macrotis* is a fast flier. Although *macrotis* has been flown successfully in a 17-m enclosed
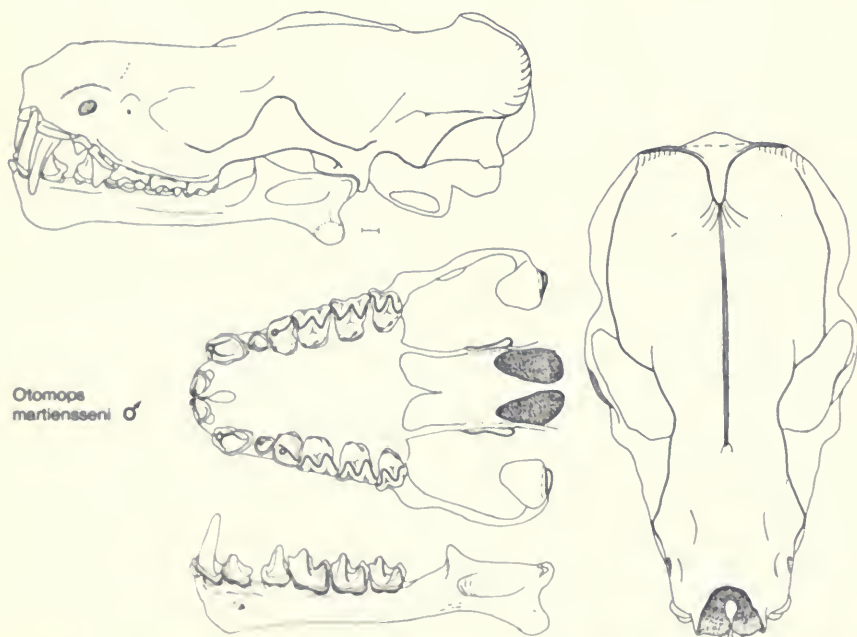
FIG. 13. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible of one species of *Otomops*.

space, it had to be launched by hand and it flew at speeds seemingly slower than those observed outside. Hayward & Davis (1964) think that because *T. macrotis* has such narrow wings it is not found in mines or caves.

There are few data on the food or flight habits of species of *Otomops*. Recently, a large colony of *O. martiensseni* was found roosting in a cave in Kenya (Mutere, 1973), and Brosset (1966) reported a colony of 40 individuals of *O. wroughtoni* in India. Brosset further noted that species of *Otomops* appear to be forest Chiroptera, unlike other molossids, and have extremely powerful flight. If cave roosting and forest-dwelling does require bats to have broader wing tips, the species of *Otomops*, rather than *T. macrotis*, may be suited for such an existence.

Species of *Otomops* and *T. macrotis* have some of the largest ears, relatively, of any molossid (0.549 correlation with axis II, table 2). The ears project forward, and Vaughan (1966) hypothesized that ears of this type may be used as additional airfoils to help keep the head aloft in flight (see also Kingdon, 1974). Also, if a relationship exists between echolocation, large ears, and deep basisphenoid pits, it has not yet been elucidated; but many of these large-eared molossids, specifically *T. macrotis*, *T. femorosacca*, *Eumops perotis*, and *E. underwoodi*, are known to emit loud low-frequency clicks. Schum (1972) has analyzed this click in *T. macrotis* and concluded that this high-intensity, low-frequency sound is most efficient for active, long-distance echoranging. A function of this nature would be appropriate for these fast-flying molossids that may not maneuver as well as bats with broader wings. It is not known whether species of *Otomops* emit these sounds, but they certainly have the same large ears and deep basisphenoid pits, the deepest of any molossid. An interesting description and discussion of the morphology of the basisphenoid pits in *Otomops martiensseni* is presented by Valdivieso et al. (1979). These authors also mention that large ears and deep basisphenoid pits seem to be correlated in molossids.

Tadarida

The bats remaining are not easily grouped by the principal components analysis, but in the distance analyses and in correlation very few species have nearest neighbors outside their genus (table 7). I lump monotypic genera with the taxa to which they are most closely related in the clustering techniques.

Species of *Tadarida* are well scattered along the negative side of axis II (fig. 4). The classical subgenus, which I presently treat as a genus, consists of species in the New World, *T. aurispinosa*, *T. brasiliensis*, *T. femorosacca*, *T. laticaudata*, and *T. macrotis*; species in Africa, *T. aegyptiaca*, and the large *T. africana*, *T. lobata*, and *T. fulminans*; species in Australia and New Guinea, *T. australis* and *T. kuboriensis*; and a species in the Palearctic, *T. teniotis*. It is the most cosmopolitan group thus far discussed and, with the possible exception of *Mormopterus*, is the most widespread genus in the family. With a wide distribution of this sort one might expect the species within the genus to be dissimilar and, hence, dispersed compared to a group that is, for the majority of species, concentrated on one continent.

All the bats on this negative side of axis II have relatively thin dentaries (fig. 4). *Otomops*, of course, has the thinnest but *Tadarida* is nearly as thin (mean relative dentary thickness is 10.0 per cent). Variation within the genus on this axis involves differing jaw proportions of dentary thickness, coronoid height,

moment arms for temporal and masseter, and height of mandibular condyle above the lower toothrow (table 6).

Variation on axis III separates most American *Tadarida* (except *brasiliensis*) from the Old World *Tadarida*. Those species on the negative side of this axis have most or all of the following characters: ears completely joined by a band superior to the rostrum, a moderately developed anterior sagittal crest, a low coronoid process, moderate to deep basisphenoid pits, and a narrow inter-orbital and lacrimal width (appendix A).

Axis IV is determined by another constellation of characters. Any variation caused by the wing characteristic is not apparent. Most New World *Tadarida* have a narrow wing tip (range of relative length of second phalanx is 3.1–4.2 per cent) but are lowered on the axis because of the codes concerning development of lateral lambdoidal crest and ear junction. Two other characteristics important on the negative end and affecting position of the narrow wing-tipped bats are relatively big ears (ear/forearm ratio) and a well developed PM³. *Tadarida kuboriensis* and *T. australis* have broad-tipped wings (relative length of second phalanx 14 per cent and 17 per cent, respectively). *Tadarida africana* is high (more positive) on axis IV because it not only has a narrow wing tip (9 per cent), but it also possesses a well-developed lateral lambdoidal crest. In these last features *africana* approaches the appearance of several species of *Eumops*.

Tadarida teniotis, the only Palearctic *Tadarida*, is in an isolated position on the far negative end of axis II, as extreme as *Otomops* and *T. macrotis*, but it is negative on axis III probably because of its wide interorbital and lacrimal width.

There appear to be groups within the cluster of species of *Tadarida* on the PCA plots that may be expected either on the basis of geographic location or because of body size. The clustering techniques place the New World *Tadarida*, with the exception of *T. brasiliensis*, close to each other (table 7). *Tadarida brasiliensis* is closer to *T. aegyptiaca* in size-out distance and correlation, but with size-in, is closest to a species of *Mormopterus* (both are small bats). A second subgrouping is among *T. africana*, *T. fulminans*, and *T. lobata*, all large African *Tadarida*. The neighbor nearest both *africana* and *lobata* is *fulminans* in all three techniques. One might suspect that the three OTU's represent fewer than three species except that the size-out distance separating them is never less than 0.432, a rather average distance in the more compact groups. Of the species remaining, the African *aegyptiaca* and the New Guinean *kuboriensis* both have different neighbors in the three analyses but both are closest to *brasiliensis* in size-out distance (table 7). *Tadarida teniotis*, found in the Palearctic region, is closest in all three techniques to the Australian *T. australis*.

Average least distance for the genus, size-in, is 0.562 which is affected, I believe, by the substantial amount of variation in the size of the species; and average least distance, size-out, for the genus is 0.458. *Tadarida* is among the dispersed groups (table 5). Among neighboring genera *Tadarida* is nearest the monotypic *Sauromys* (0.711), followed closely by *Chaerephon* (0.743) and then by *Mormopterus* (0.799) and *Otomops* (0.829). The farthest neighbor of *Tadarida* is *Cheiromeles* at a distance of 1.441 (table 8). These neighbors correspond well with the positioning in the principal components analysis (fig. 4).

Greatest skull lengths of *Tadarida* range from 16.5 mm in *brasiliensis* to 24.0 mm in *teniotis* and *africana*. Shapes in the skulls of Old World *Tadarida* do not show predictable change as size increases as do skulls of *Mops* and *Molossus* and, for that matter, New World *Tadarida* (figs. 14, 15).

Because the structure of the jaws in *Tadarida* is much like that of *Chaerephon* and *Otomops*, I suspect that the functional capabilities of the jaws are much the same. *Tadarida* probably concentrates on soft-bodied prey and, indeed, what data there are support this prediction. In the New World species, *brasiliensis*, *femorosacca*, and *macrotis* (see preceding account), a large percentage of their diet consists of moths. *Tadarida femorosacca*, like *macrotis*, is capable of taking Macrolepidoptera (100 per cent in one stomach) but has also taken Microlepidoptera and Coleoptera (85 and 15 per cent, respectively, in one stomach; Ross, 1967). Easterla & Whitaker (1972) reported that in 13 *femorosacca* large moths made up 36.9 per cent of the volume in 69.2 per cent of the stomachs. They also found lesser percentage volume and frequency of many other flying insects (Formicidae as well as Hymenoptera, Hemiptera, Diptera, and Coleoptera) and of unlikely things such as Gryllidae, Tettigoniidae, Cercopidae, and Cicadellidae; all terrestrial insects which were thought to have been captured in the roosts.

Tadarida brasiliensis, a common molossid, has been much studied. Ross (1967) reported this small bat taking prey from 2-10 mm in length and gave the following proportions of food items for 88 specimens: Lepidoptera, 34 per cent; Hymenoptera, 26.2 per cent (flying ants); Coleoptera, 16.8 per cent (scarabs and chrysomelids); Homoptera, 15 per cent; and Hemiptera, 6.4 per cent. A report by Bailey (1931) indicated this species to have taken 95 per cent moths and 5 per cent mixed insects, and Storer (1926) reported over 90 per cent moth material. Sherman (1939) noted that six of eight *Tadarida cynocephala* (=*T. brasiliensis cynocephala*) had eaten Lepidoptera whereas none were found in three vespertilionids (*Lasiurus*, *Dasypterus*, and *Pipistrellus*). He went further to say that two of the eight contained Homoptera; one, Odonata; one, Neuroptera; six, Diptera; four, Coleoptera; and six, Hymenoptera. Ross (1967) mentioned that *brasiliensis* feeds in groups of 10-13 individuals and often prey on densely swarming insects, a foraging method which he calls filter feeding. Vaughan (1966) suggested that such molossids with wrinkled lips fly through the air with their mouths open using their expandable wrinkled lips as a funnel much like the rictal bristles around the mouths of caprimulgiform birds.

My own data from fecal samples of *T. brasiliensis* show only one sample to have many thousands of moth scales present and four others from a different locality to have only one to three thousand scales (table 9). Some dipteran and other non-moth parts were present. It may be that this bat takes whatever prey species is abundant and because of its small size is capable of taking hard as well as soft items. A similar diversity of prey occurs with *Molossus coibensis* where it seems to be taking soft as well as hard items.

At present there are few food data for the Old World species of *Tadarida*. As mentioned previously *ansorgei*, either a species of *Tadarida* or *Chaerephon*, has been found with remains of Formicidae, other Hymenoptera, and Coleoptera in its stomach (Verschuren, 1957).

The New World *Tadarida* (except *T. brasiliensis*), with their narrow wing tips, are probably faster and less maneuverable than most of the Old World species. There are no quantitative data on flight in the Old World *Tadarida*, but Findley et al. (1972) estimate speed of flight in some of the New World species based on surface area of the flight membranes and weight of the bats. Those authors project a speed in *brasiliensis* as being 24 m.p.h. and speed in *femorosacca*, *macrotis*, and *Eumops underwoodi* of 27 m.p.h. These were all thought to be

Tadarida brasiliensis ♂
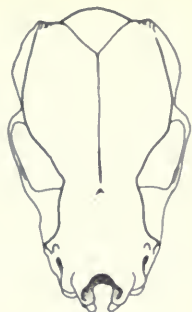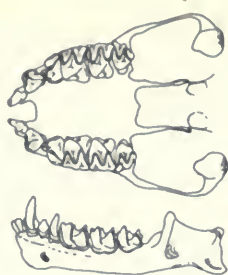
Tadarida aegyptiaca ♂
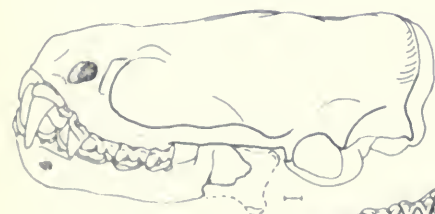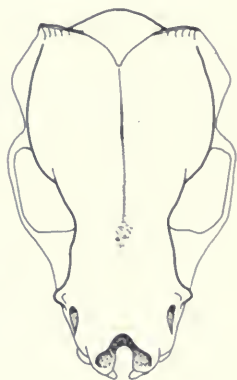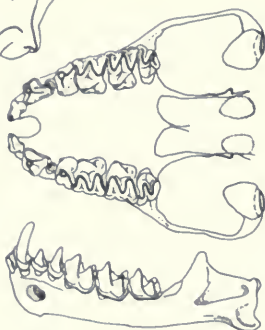
Tadarida lobata ♀

FIGURE 14.

70
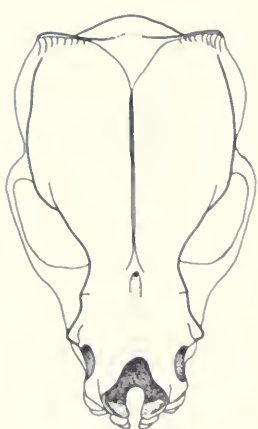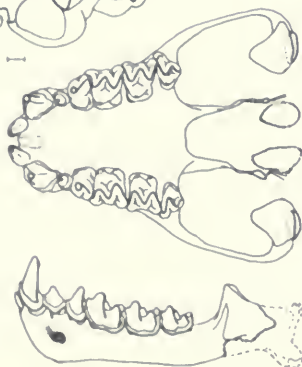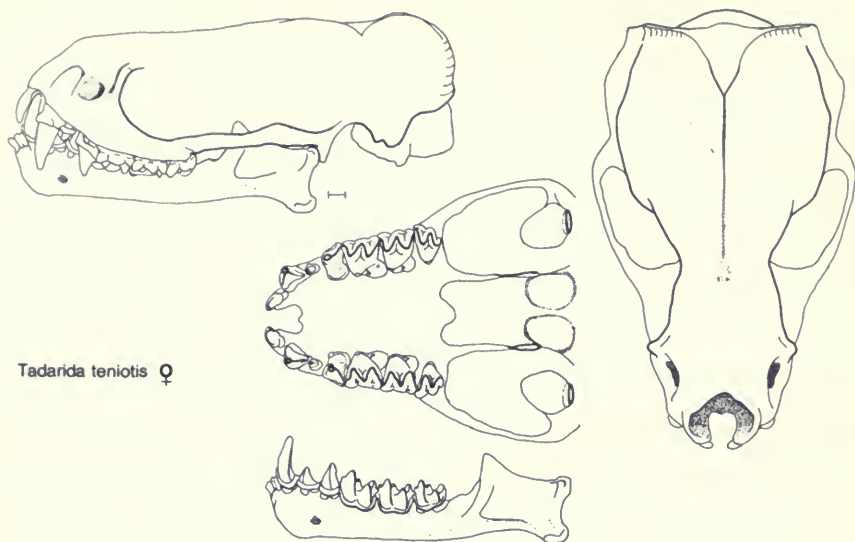
Tadarida teniotis ♀
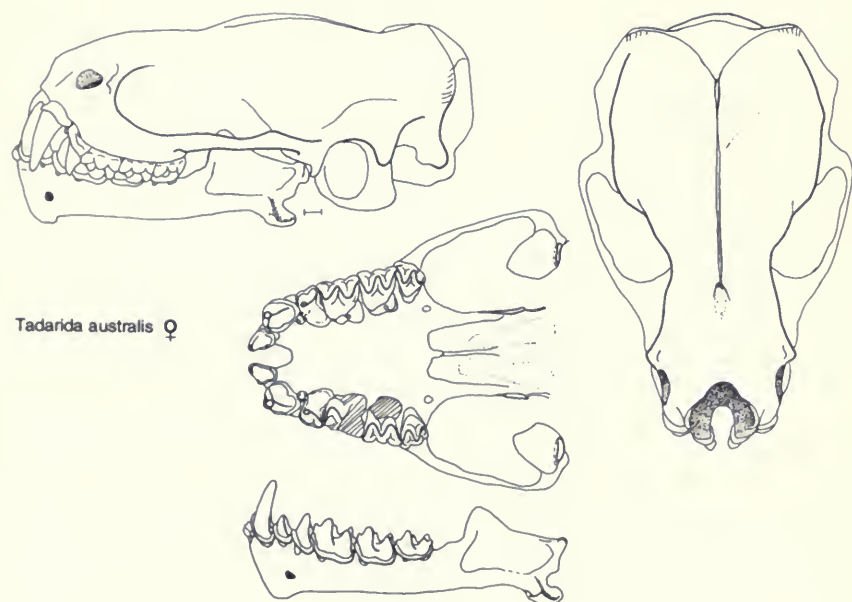
Tadarida australis ♀

FIGURE 14.

71

Tadarida africana ♂
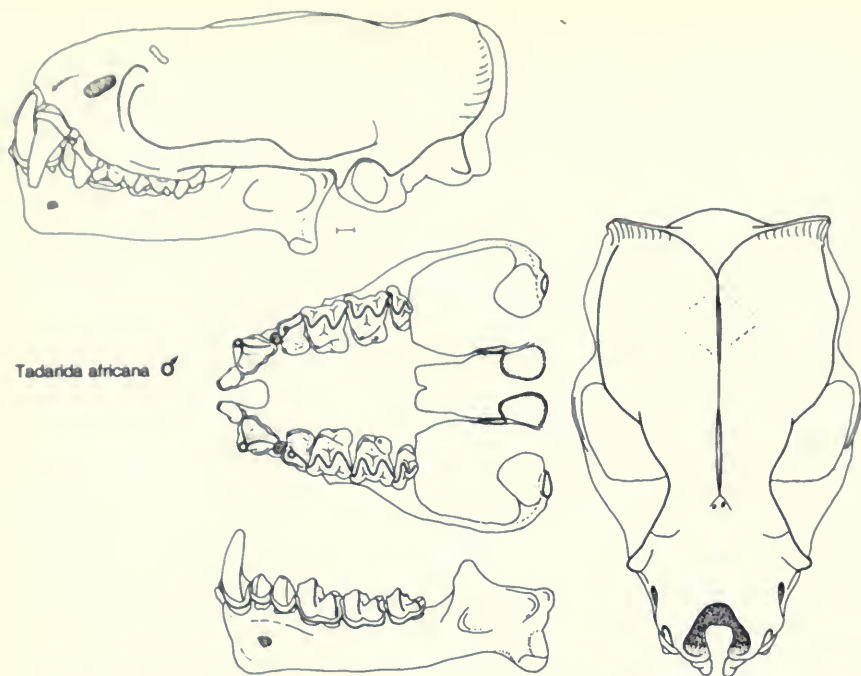
FIG. 14. Six species of *Tadarida* arranged from small to large. Lateral, dorsal, and occlusal view of the skulls and lateral view of the mandibles are given for all six.

underestimates. Allison (1937) calculated a speed of 20 m.p.h. in *brasiliensis*, whereas Hayward & Davis (1964) estimated 10-20 m.p.h. My own observation of *brasiliensis* is that it is not only able to fly in a room with little trouble (it does not crash into walls and can take off from the floor), but it is also very maneuverable. Ross (1967) observed *T. brasiliensis* foraging with the fluttery small pipistrelles. Others have observed that the larger *femorosacca*, *macrotis*, and *Eumops perotis* rarely can take flight in a room and usually crash into a wall if they do (Krutzsch, 1955; Hayward & Davis, 1964). I have successfully launched and seen *macrotis* fly in a 17-m room, although at slow speeds. Vaughan (1966) calculated that *T. brasiliensis* has a lower aspect ratio, and thus slower speed, than *T. macrotis*. A slower speed is supported in this study by the fact that *brasiliensis* has a broader-tipped wing than *macrotis* (table 4).

Tadarida femorosacca and *T. macrotis* are usually found in high places like cliffs and rock crevices, whereas *T. brasiliensis* is found in those places as well as in caves and more enclosed areas (such as roofs of houses). Two of the three, along with a large species of *Eumops*, may be found in the same crevice, but the smaller bats stay in narrow peripheral portions and the larger ones in wide central portions (Krutzsch, 1955). *Tadarida aurispinosa* has been taken in the Bogota Savannah (Tamsitt et al., 1964) and *T. laticaudata* has been taken from a palm 13 m high (Silva-Taboada & Koopman, 1964) and from man-made structures in the lowlands of Guatemala (Jones, 1966). Koopman (personal communication) has seen a large colony of *T. laticaudata europs* in a church in the province of Rondonia in Brazil.

There are few data on the habits of African or Australasian molossids or even on the Palearctic *T. teniotis;* however, some information exists on roosting places of these bats and places of capture. The three large *Tadarida* in Africa are thought to live in cliffs or high rocky places, situations where *T. lobata* and *T. fulminans* have been found. The latter two seem to prefer arid or semi-arid plains (Peterson, 1974). Little is known about *africana* but it has, along with *fulminans,* the narrowest wing tips of the Old World *Tadarida* (relative length of second phalanx is 9.0 per cent). *Tadarida aegyptiaca* has been found in caves and in large buildings (Rosevear, 1965), under stone slabs on a hillside, along with *Sauromys* (Irwin & Donnelly, 1962); and inhabits arid regions in East Africa (Brosset, 1963). The Australasian *kuboriensis* and *australis* have the broadest wing tips in the genus. The former has been found at 2,750 m in *Nothofagus* and moss forest (McKean & Calaby, 1968), and the latter frequents open places where it has been caught in windmill blades some 12 m off the ground (Hall & Richards, 1972). Dwyer (1965) noted that *australis* can launch itself from a rough horizontal surface with great difficulty but cannot maintain flight in a room 7.6 by 4.6 m.

Recently, Vestjens & Hall (1977) reported on the stomach contents of 21 specimens of *Tadarida australis.* There were 20 occurrences of moths, two of scarabs, one of ants, two of unidentified Hymenoptera, and one of unidentified Hemiptera. No remains of water beetles were found as Shortridge (1936) had suspected, but there was a dominance of moth remains.

Bats on the negative end of axis II tend to have larger ears (fig. 4). A few bats on this end also have a loud click which may be related to long-distance echo-ranging (Schum, 1972). Krutzsch (1944) noted a high-pitched, sharp call in *T. femorosacca,* whereas Peterson (1974) reported that *T. lobata* emits a distinctive single or double-noted loud squeak. Perhaps significantly, all these large-eared, loud-clicking bats (*T. macrotis, T. femorosacca, T. lobata, E. underwoodi,* and *E. perotis californicus*) have deep basisphenoid pits, are found in arid regions, and are considered cliff dwellers.

Mormopterus-Sauromys-Platymops

The fourth and last classical subgenus of *Tadarida* is *Mormopterus,* the species of which are scattered but are generally located in the middle of axis II in the PCA plots (fig. 4). *Mormopterus,* like *Tadarida,* is found on several continents: *M. kalinowskii* and *M. phrudus* are from Peru, and *M. minutus* is from Cuba; *M. jugularis* and *M. acetabulosus* are from Africa and Madagascar; and *M. beccarii, M. loriae, M. norfolkensis,* and *M. planiceps* are from the Australia-New Guinea area. These last three may be taxonomically confused. If the monotypic African genera *Sauromys* and *Platymops* are added to this group, the dispersion is only slightly greater (table 5). Both ordination and clustering procedures indicate a relationship between these two monotypic genera and *Mormopterus.*

Most variation occurring in these bats is along axis II or the jaw axis. Average relative dentary thickness is about 11 per cent (range from 9.3-14.5 per cent), a mean similar to that of *Chaerephon.* Average height of mandibular condyle is higher than that in any group except *Cheiromeles* (mean relative condylar height is 15.6 per cent, *Sauromys* is less here). All have a well-developed posterior commissure on M^3, but few retain PM^3 (if present it is usually small); a combination which is somewhat unusual in that the two traits are usually present or absent together (table 6, appendix A). *Mormopterus beccarii* is extreme in all of

Nyctinomops laticaudata ♂
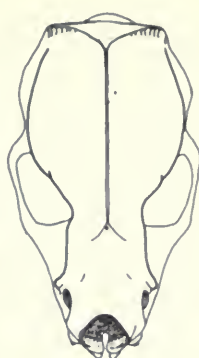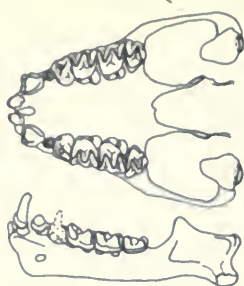
Nyctinomops femorosacca ♂
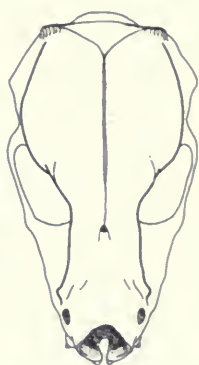
Nyctinomops aurispinosa ♂

FIGURE 15.

74
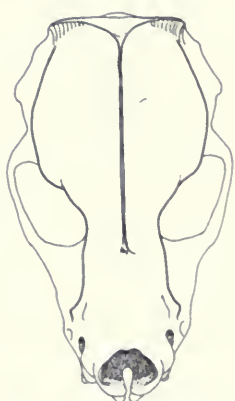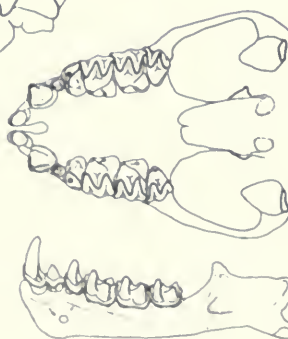
the characters highly correlated with this second principal component. It has a very thick dentary, very high coronoid and condyloid processes, and the largest relative temporal and masseter muscle moment arm index. This bat is also the largest of the group, making it an extreme not only in shape but also in size (fig. 16).

The positions of these bats on the two other axes, III and IV, are not as strikingly variable (fig. 4). As a group, *Mormopterus*, *Platymops*, and *Sauromys* have widely separated small ears (less so for *Sauromys*), shallow or nonexistent basisphenoid pits, little or no wrinkling on the lips, no development of the anterior sagittal crest, a high coronoid process, and a wide face (interorbital and lacrimal breadths). These are all characters which position the group as one of the most positive on axis III. On axis IV variation among the first five or six pertinent characters is such that the bats tend to be grouped around the mid-point of the axis. One interesting occurrence is that *beccarii* has unusually large ears that perhaps causes it to occupy a negative position on this axis. The bats have a relatively broad wing with mean relative length of second phalanx of 15.0 per cent and range from 9.4-18.8 per cent. *Mormopterus phrudus* and *Sauromys* have narrowest wing tips; and *Playmops* and the three Australian *Mormopterus* have the broadest wing tips.

The clustering techniques reveal that all nearest neighbors or highly positively correlated neighbors are within the genus and, as mentioned earlier, nearest neighbors of *Sauromys* and *Platymops* are species of *Mormopterus* (table 7). *Platymops* is nearest *Sauromys* only in the size-in analysis. In both shape analyses *Platymops* is closest to *Mormopterus acetabulosus* in distance (0.673, a substantially great distance, to be sure) and in correlation (0.622). The neighbor, *acetabulosus*, is found on Mauritius and in southeastern Sudan and is sympatric with *Platymops* in southwestern Ethiopia. The South African *Sauromys*, on the

Nyctinomops macrotis ♀
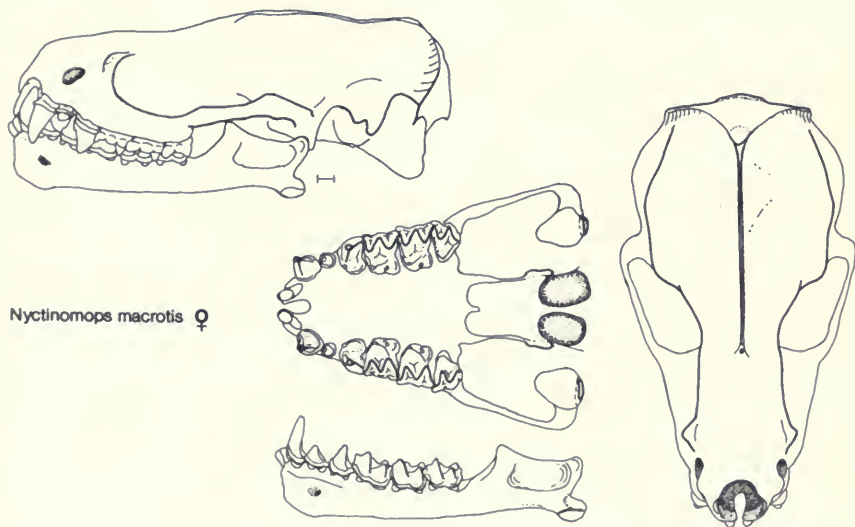
FIG. 15. Four species of *Nyctinomops* (New World *Tadarida*). Lateral, dorsal, and occlusal view of the skulls and lateral view of the mandible are given for all four. Use of the name *Nyctinomops* (Miller, 1902) is explained in the Evolutionary Relationships section.

Mormopterus (Mormopterus) minutus ♂

Mormopterus (Mormopterus) loriae ♂
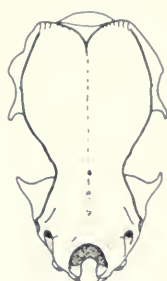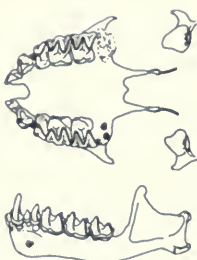
Mormopterus (Mormopterus) norfolkensis ♀
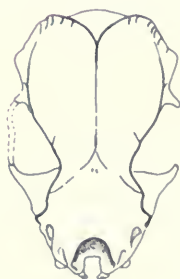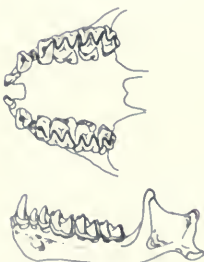
Mormopterus (Mormopterus) kalinowskii ♂

FIGURE 16.

76

Mormopterus (Mormopterus) planiceps ♀
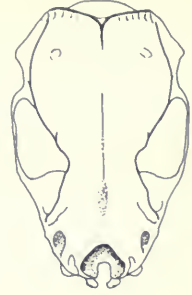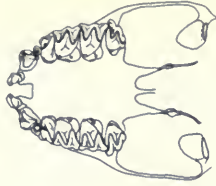
Mormopterus (Mormopterus) phrudus ♂
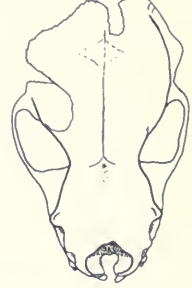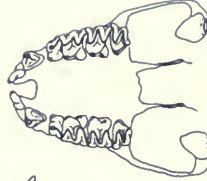
Mormopterus (Mormopterus) jugularis ♀
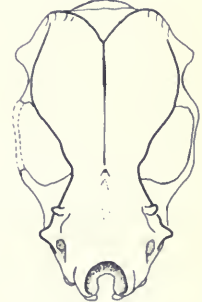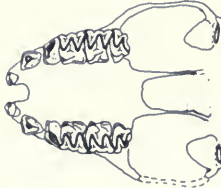
Mormopterus (Mormopterus) beccarii ♂

FIGURE 16.

77
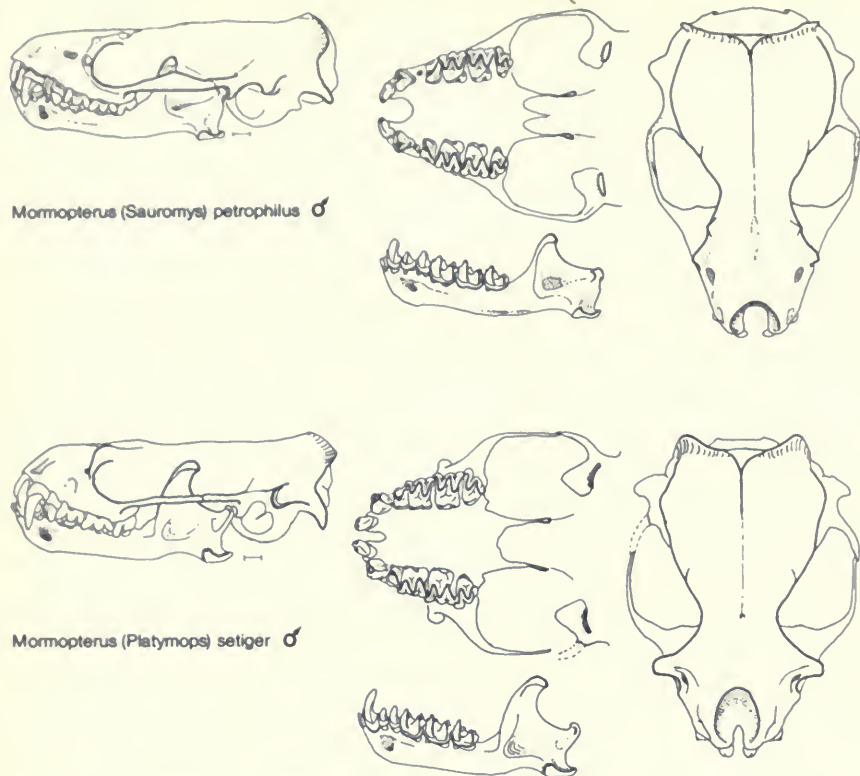
FIG. 16. Ten species of *Mormopterus*, including *Sauromys* and *Platymops*. Lateral, dorsal, and occlusal views of the skulls and lateral view of the mandibles are given for each species. The treatment of *Sauromys* and *Platymops* as subgenera is explained in the Evolutionary Relationships section.

other hand, is closest in all three analyses to *Mormopterus norfolkensis* (size-in distance of 0.570, size-out distance of 0.448, and correlation of 0.663), a bat found many miles away on the Cape York Peninsula in Australia.

Within *Mormopterus* the New World representatives are nearly always closest to each other. Only in the correlation analysis is *minutus* most highly correlated with *norfolkensis*. These New World species, *kalinowskii*, *minutus*, and *phrudus*, form a compact group among themselves with size-out distances of less than 0.340. The Australian *Mormopterus* form another tightly bound group in which *loriae*, *norfolkensis*, and *planiceps* are nearest neighbors to one another in all three clustering methods and have no greater size-out distance among them than 0.400. I suspect there may actually be fewer than three species involved in each of these two compact groups of *Mormopterus*, because each has a pair of bats joined at a size-out distance of less than 0.300, a small distance in this analysis.

Mormopterus beccarii from New Guinea and the Moluccas is a distinctive bat in both size and shape and like *Sauromys* and *Platymops* is somewhat distant from other *Mormopterus* species. It is nearest in distance to *jugularis* from

Madagascar (size-in of 0.658 and size-out of 0.595) as well as being most highly correlated with it (correlation of 0.701). *Mormopterus jugularis*, on the other hand, is nearest the Australian *norfolkensis* in both distances but most correlated with the Neotropical *phrudus*. The other Malagasy (and African) *Mormopterus*, *acetabulosus*, is nearest New World species *minutus* in both distances and *kalinowskii* in correlation only.

Though dispersed in the PCA, species of *Mormopterus*, even including the outlying genera, *Platymops* and *Sauromys*, fall on the compact side of least averages within taxa both in size-out and size-in distance (table 5). Nearest neighbors among genera to *Mormopterus* alone are *Sauromys* (0.570), *Molossops* (0.706), and *Neoplatymops* (0.721); farthest are *Otomops* at 1.100 and *Cheiromeles* at 1.023. *Sauromys* is closest to *Mormopterus* (0.570), then to *Tadarida* and *Platymops* (0.711), and farthest from *Cheiromeles* (1.154); *Platymops* is closest to *Neoplatymops* (0.700), *Sauromys* (0.711), *Molossops* (0.737), and *Mormopterus* (0.752) and farthest from *Otomops* at 1.290 (table 8).

Bats of this group are small in size for molossids. Greatest skull lengths range from 13.4 mm in *minutus* to 18.4 mm in *beccarii* including *Platymops* (15.5 mm) and *Sauromys* (17.6 mm, table 1). All species of *Mormopterus* have a similar appearance in that they all possess a delicately shaped and tall coronoid process. The two flat-headed bats *Sauromys* and *Platymops* are similar in this regard (fig. 16). Height of the coronoid may be related to different leverage for the temporal muscle, making the direction of pull directly posteriad rather than posterio-dorsad. This change in temporal muscle force occurs in shrews to an advanced degree and is thought to cause the shift in contact from the superior condylar facet to the inferior condylar facet (Fearnhead et al., 1955). If all the bats in this group are considered flat-headed (to a lesser or greater degree), then the increased height in the coronoid process would compensate in leverage for a temporal muscle that has been forced to extend laterally. The greatest development of the lateral lambdoidal crest is in the African flat-headed bats, *Platymops* and *Sauromys* (also *M. jugularis*), whereas most of the other *Mormopterus* bear a crest only moderately developed. Flat-headedness occurs in several molossids and is thought to be a result of living in very narrow crevices (Peterson, 1965). All of the so called flat-headed bats, *Sauromys*, *Platymops*, and *Neoplatymops*, are phenetically related to *Mormopterus*. Not only is the coronoid process high in these bats, but the mandibular condyle is well elevated above the toothrow. I think this last feature gives some undetermined advantage to the jaw action, an advantage which could be very helpful for small bats with relatively thin dentaries.

Of all molossids, bats of the genus *Mormopterus* are the least known because there are few specimens of species in this genus and little has been written about them. Specimens of *Platymops* and *Sauromys* may be slightly better represented in collections. Likewise, little food and flight data are available for these bats.

With the exception of *M. beccarii* and possibly *M. jugularis*, I think this group of bats may be eating small-sized, soft-bodied prey. However, if the elevated mandibular condyle is imparting an advantage in mastication and small-sized bats are relatively stronger, I believe these bats could be taking hard items as well as soft. Evidence in support of this last idea recently came to my attention when I had a chance to make a qualitative examination of stomachs of 11 *Sauromys* (specimens at the Los Angeles County Museum). The stomachs con-

tained Coleopteran remains, some moth scales, and non-moth and non-beetle remains. *Mormopterus beccarii*, because of its heavier build, could probably take more heavily armored and larger insects. Vestjens & Hall (1977) reported on the stomach contents of *Tadarida planiceps* (=*Mormopterus*) and *T. loriae* (=*Mormopterus*). In the 17 specimens of *planiceps* there were 10 occurrences of Lepidopteran remains, eight of Coleopteran remains (one each of Carabidae, Dysticidae, Scarabaeidae, and Curculionidae, and four unidentified), eight of Hymenopteran remains (seven of Formicidae and one unidentified), five of Hemipteran remains (two Pentatomidae and one unidentified), one of Insecta (Blattodea), and one of unidentified insects. This evidence seems to support my ideas presented above.

All but *M. phrudus* and possibly *Sauromys* have broad wing tips, and I suspect they are more maneuverable in flight than most other molossids, especially because of their small size. If roosting places are any evidence at all for support or nonsupport of flight activity in bats, then the following notes are necessary. *Mormopterus minutus* has been found in a "rather tall palm" (Silva-Toboada & Koopman, 1964, estimates 13 m), *Copericia vespertilionum*, in open savannah country which contained scattered clumps of scrub and palmettos (Sanborn, 1953). *Mormopterus norfolkensis* has been found roosting in buildings; *M. planiceps*, in hollow trees (McKean & Hamilton-Smith, 1967); and *M. loriae*, in roofs of houses (McKean & Price, 1967). *Sauromys* has been found in association with *T. aegyptiaca bocagei*, a small subspecies, along the Limpopo river in Southern Rhodesia (Irwin & Donnelly, 1962). This is a riparian situation, but it is a hot dry river valley of the low veld containing sandstone cliffs and acacia trees. Both bats were found under sandstone slabs on hillsides during the day. At night *Sauromys* and a large *Tadarida* were flying as high as 37 m. *Sauromys* has been found in the very dry Namib desert in southwestern Africa and has been known to live on insects and no additional water (Roer, 1971). The insects in the area (dry river beds) were Coleoptera, Lepidoptera, and Hymenoptera. Bruce Hayward (personal communication) stated that *Platymops* and *T. aegyptiaca* are often found in the same places in Kenya, namely in dry areas under flakes of rocks.

Molossops-Neoplatymops-Cynomops-Myopterus

The four remaining genera in the immediate vicinity of *Mormopterus* in the PCA plots are *Molossops*, *Neoplatymops*, *Cynomops*, and *Myopterus* (fig. 4). All are genera with one, two, or three species and together form a somewhat diffuse conglomerate on the positive side of *Mormopterus* and on the more positive end of axis II. *Molossops*, *Neoplatymops*, and *Cynomops* are New World and mostly South American; while *Myopterus* is from Africa. Bats in this group tend to have thickish dentaries and broad faces (figs. 17, 18). All have widely separated ears, no anterior sagittal crest development, no anterior palatal emargination, and no development of wrinkles on the lips. They have no development of the basisphenoid pits except for *Myopterus*, which has very deep ones (table 6, appendix A).

The smallest species in this conglomerate and among the smallest species in the family are two South American genera, *Molossops temminckii* and *Neoplatymops mattogrossensis* (fig. 17).

Molossops temminckii is the smallest bat in the study (GSL = 13.2 mm, table 1). It is medium in most jaw proportions (relative dentary thickness is 12 per cent,

table 6), but its mandibular condyle is elevated above the toothrow more than in any other molossid (relative height is 20.0 per cent), its ears are separated, its basisphenoid pits are nonexistent, its lips are without wrinkles, and its wing tips are broader than in any other molossid (relative length of second phalanx is 20.0 per cent).

Molossops is clustered nearest *Neoplatymops* in all three analyses but its next nearest neighbor in size-in and correlation is *Mormopterus loriae* and in size-out is *Cynomops planirostris* (table 7). The PCA distorts the relationship between these closest neighbors. The size-out distance of 0.491 between *Molossops* and *Neoplatymops* places the two among the dispersed averages in Table 5, but at a distance which separates two species much less two genera, the figure is not great and is actually less than the one separating the two species of *Myopterus*. Nearest neighboring genera (table 8) after *Neoplatymops* are *Cynomops* at 0.579, *Myopterus* at 0.618, *Promops* at 0.704, and *Mormopterus* at 0.706. The farthest genus from *Molossops* is *Otomops* at 1.262.

Neoplatymops mattogrossensis, another small bat with a GSL of 13.9 mm, is similar to *Molossops* except that its jaw proportions are even more like those in *Mormopterus* including a thinner dentary and higher coronoid process (fig. 17). *Neoplatymops* has a very elevated jaw joint (relative condylar height is 18.6 per cent) like that of *Molossops* but its wing tips are less broad (relative length of second phalanx is 12.3 per cent) than those of *Molossops* (table 5); its ears are separated, but it has shallow basisphenoid pits and its lips appear slightly wrinkled. Other individualistic features are an almost complete posterior commissure on M^3 (*Molossops* has less than one-half of the cusp present), a vestigial PM^3 (other conglomerate members have none), and the largest ears, relatively, of any other species in the conglomerate. These last features are very like those of *Mormopterus*, and the only difference apparent is that *Neoplatymops* completely lacks the palatal emargination, whereas *Mormopterus* has a well-developed one.

Neoplatymops is nearest *Molossops* in all three clustering analyses (table 7), and its next nearest species in all analyses is *Mormopterus minutus*, another very small bat (GSL = 13.4 mm).

Besides *Molossops*, the next nearest taxa are *Cynomops* at 0.640, *Myopterus* at 0.668, and *Mormopterus* at 0.681 (table 8). I think this latter neighbor is not nearer as one might expect, because the first average is made from only three rather similar species of *Cynomops*, the second average from only two species of *Myopterus*, and the third is made from seven rather divergent species of *Mormopterus*.

Jaws in *Molossops* and *Neoplatymops* have the combined qualities of both *Cynomops* and *Mormopterus*, namely moderately thick jaws and well-elevated condyles above the toothrow, respectively. With the strength of the first and the possible mechanical advantage of the second, these little bats may well be able to eat both hard and soft-shelled items within their size range. *Neoplatymops* is one of the flat-headed bats (Peterson, 1965) and has a relatively high coronoid process (like that in *Sauromys*), which as mentioned in the *Mormopterus* account, may be related to a lateral shift in the location of the temporal muscle on the flattened skull. Food data for *Molossops* and *Neoplatymops* are nonexistent.

Likewise, no data exist for the speed of flight or the maneuverability of these two bats. *Molossops* has been found in decaying wood of a log (Walker, 1975) that may have been in a forest of some sort. Fenton (1972) reported that Neo-

Molossops (Molossops) temminckii ♀
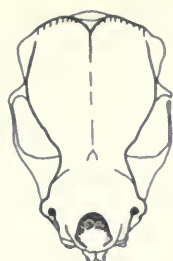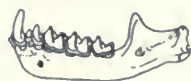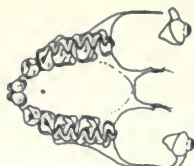
Molossops (Neoplatymops)
    mattogrossensis   ♂
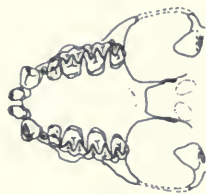
Molossops (Cynomops) planirostris ♂
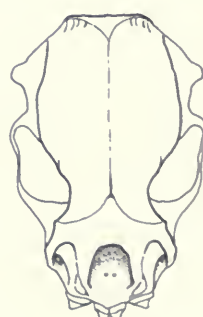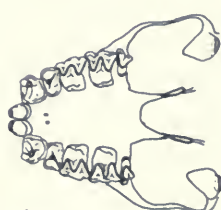
Molossops (Cynomops) greenhalli ♂

Figure 17.

82

Molossops (Cynomops)
brachymeles ♀
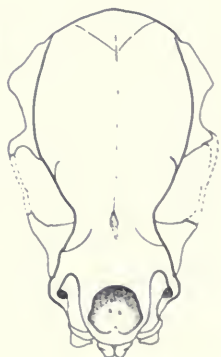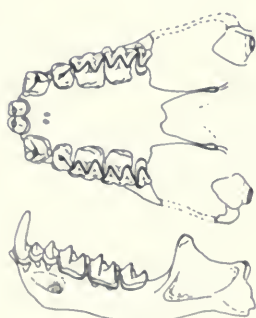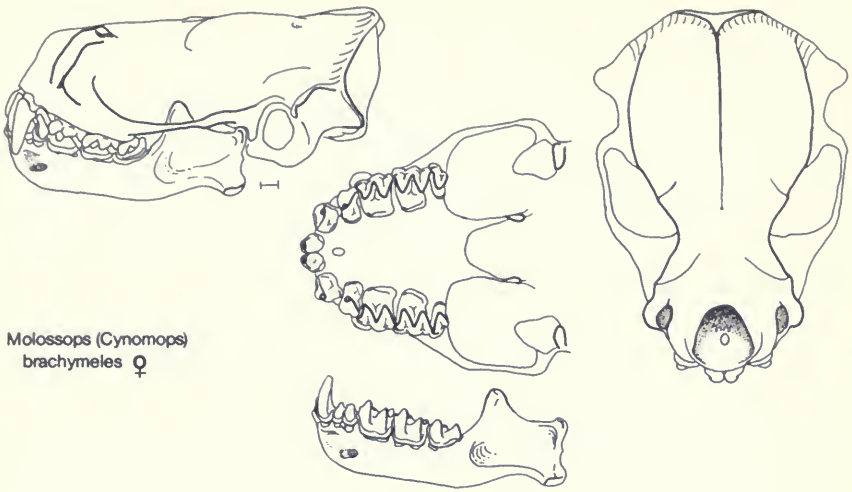
Fig. 17. Five species of *Molossops*, including *Neoplatymops* and *Cynomops*. Lateral, dorsal, and occlusal views of the skulls and lateral view of the mandibles are given for each species. The treatment of *Neoplatymops* and *Cynomops* as subgenera is explained in the Evolutionary Relationships section.

Myopterus albatus ♀
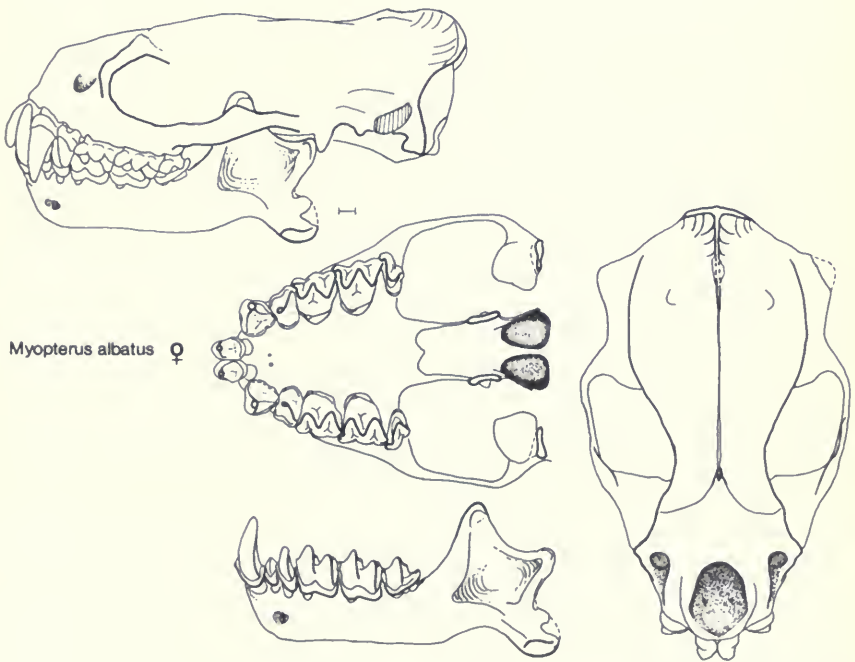
Fig. 18. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible of one species of *Myopterus*.

tropical species of *Molossops* along with three other molossids are caught only in the canopy. *Neoplatymops* has been found "underneath a stone out in the savannahs" of British Guiana (Peterson, 1965) and at "the edge of a small lagoon in an area made up of stone ledges, sparsely covered by a shrubby xerophytic vegetation called 'caatinga'," in eastern Brazil (Sazima & Taddei, 1976). These authors suspect that, with roosts at ground level, *Neoplatymops*, in order to take flight, "may require a flight capacity not generally seen in molossids." I doubt that *Neoplatymops* is unusual in its flying ability because I have seen *Tadarida brasiliensis*, a larger bat but one with similar wing tips (relative length of second phalanx of 12.0 per cent), take off readily from the ground.

Species of *Cynomops*, *C. brachymeles*, *C. greenhalli*, and *C. planirostris*, have slightly thicker jaws than those in *Mormopterus* (mean relative dentary thickness is 12.3 per cent), shorter coronoid processes, and a slightly less elevated mandibular condyle (mean relative height of condyle is 14.5 per cent). The three species have completely lost the PM^3 and posterior commissure on M^3. Combining these features with the absence of a palatal emargination and presence of sturdy beaklike incisors makes *Cynomops* much like *Molossus* and unlike the variable *Mormopterus*. Wing tips are narrow (mean relative length of second phalanx is 7.6 per cent), but this feature is obscured on axis IV. The large *Cynomops brachymeles* is a robust bat, larger than the largest *Mormopterus* and reminiscent of the larger *Myopterus*; whereas the smaller *C. greenhalli* has features closer to *Mormopterus* (for example, relative dentary thickness is only 11.3 per cent; fig. 17). The three species of *Cynomops* in the PCA plots (fig. 4) are equidistant, ignoring the immediate conglomerate members, from *Molossus*, *Mops*, and *Mormopterus* and have morphological features similar to all three.

Clustering techniques among species of *Cynomops* are no more definitive as to which group of bats are nearest to them. Size-in distances indicate that the large *C. brachymeles* is closer to the larger, thick-jawed bats of *Molossus*, *Mops*, *Promops*, and *Eumops*, whereas the two smaller-sized species of *Cynomops* are closer to the smaller *Mormopterus* and *Molossus* (table 7). The average least distance within genus (size included) is 0.570, making it third from the most dispersed taxa (table 5). Variation in size greatly affects this figure.

Size-out distances correspond well with the PCA model. Nearest neighbors of *Cynomops* in this analysis are congeners, large and small. The size-out average least distance within genus is 0.304, which is low, and makes the genus very compact, second only to *Cheiromeles* at 0.278 (table 5). Summarily, species of *Cynomops* are very similar in shape to one another.

The correlation analysis places species of *Cynomops* as most highly correlated with one another. After congeners, the neighbor most highly correlated with *C. brachymeles* is *Cheiromeles parvidens*; and the neighbor most highly correlated with *C. planirostris* is *Molossops temminckii* (table 7).

Among genera in the family, *Cynomops* is closest to genera in the conglomerate: *Molossops* at 0.579, *Neoplatymops* at 0.640, and *Myopterus* at 0.720. Closest taxa outside the conglomerate are *Mops* at 0.756 and *Mormopterus* at 0.761. The farthest neighbor from *Cynomops* is *Otomops* at 1.278 (table 8).

The species of *Cynomops* are small to medium in size: *planirostris* has a GSL of 15.4 mm; *greenhalli*, 17.4 mm; and *brachymeles*, 20.4 mm. Ecologically, I think *Cynomops* is swift flying for molossids and is endowed with medium-strong jaws. Fecal analysis of one *C. greenhalli* (table 9) showed no moth scales present, and the only cuticle remains were those of beetles. Walker (1975)

mentioned that this species in captivity took only flying termites, and that normally it roosted in hollow branches of large trees (*Tabebuia serratifolia* for one; Goodwin, 1958). *Cynomops greenhalli* has been captured over a small stream in "dense tall tropical deciduous forest" (Jones & Genoways, 1967), over a small pond just below a pine-oak zone, and over a pond and fast-running stream in dense forest (Jones & Dunnigan, 1965). LaVal (1969) reported taking *greenhalli* over a small stream bordered by low gallery forest and coffee fincas and again from tropical lowland rain forest consisting of banana groves, second growth and botanical gardens. Fenton (1972) wrote that species of *Cynomops* and *Molossops* were caught only in upper levels of the canopy. Little else is known about *Cynomops*.

The final genus within the conglomerate group is *Myopterus*, an African genus of two species widely separated by size (fig. 19). Greatest skull length in *M. whitleyi* is 17.3 mm, whereas in *M. albatus* it is 23.5 mm (table 1). As a member of the conglomerate, *Myopterus* occupies the same general place on axis II; toward the thick-jawed, negative end (fig. 4). Though similar in condylar height above the toothrow (mean relative height is 14.0 per cent) the other jaw proportions of the two species are very divergent. The large *M. albatus* has a relatively thicker dentary (13 per cent versus 10 per cent in *M. whitleyi*), higher coronoid process (39 per cent versus 34 per cent, respectively), and greater temporal and masseter muscle moment arms (67 per cent versus 57 per cent, respectively; see table 6 for comparisons with other bats). Both *Myopterus* have broad wing tips (mean relative length of second phalanx is 17.0 per cent), and both have lost PM^3 and the posterior commissure on M^3. Like the other bats in the conglomerate group, these two have separated ears and unwrinkled lips; but unlike the others, the two species of *Myopterus* have deep basisphenoid pits.

The size-out distance analysis is only one of the three clustering analyses that places the two congeners as each other's nearest neighbor. The intra-generic distance, 0.528, places *Myopterus* among the dispersed groups (table 5). Each has *Molossops temminckii* as its next nearest neighbor in this analysis.

Size-in analysis indicates that the large *Myopterus albatus* is closest to *Mops niangarae* at 0.757, and *Myopterus whitleyi* is closest to *Cynomops greenhalli* at 0.615. The size-in intra-generic distance is 1.489, the highest figure in table 5. Correlation between congeners is only 0.459. *Myopterus albatus* is most highly correlated with *Cheiromeles parvidens* at 0.476, whereas *M. whitleyi* is most highly correlated with *Molossops temminckii* at 0.555 (table 7).

Among genera, *Myopterus* is nearest *Molossops* at 0.618, *Neoplatymops* at 0.668, *Cynomops* at 0.720, and then to *Mops* (0.792) and *Mormopterus* (0.788); farthest neighbor is *Otomops* at 1.270 (table 9).

The two species of *Myopterus* are divergent not only in size but also in shape. A size-out distance of 0.528 is great for similarly shaped bats. Probably, *M. albatus* is able to consume large hard-bodied prey, while *M. whitleyi* is capable of consuming small, soft-bodied prey. No food data are available. In flight they are probably more maneuverable than most molossids and possibly slower. *Myopterus whitleyi* is known to be a species of the high forest and roosts in vegetation and sometimes houses (Rosevear, 1965). Lang & Chapin (1917), with some question, placed *M. albatus* in a group of forest species; but Hayman & Hill (1971) reported that *M. albatus* inhabits savannahs.
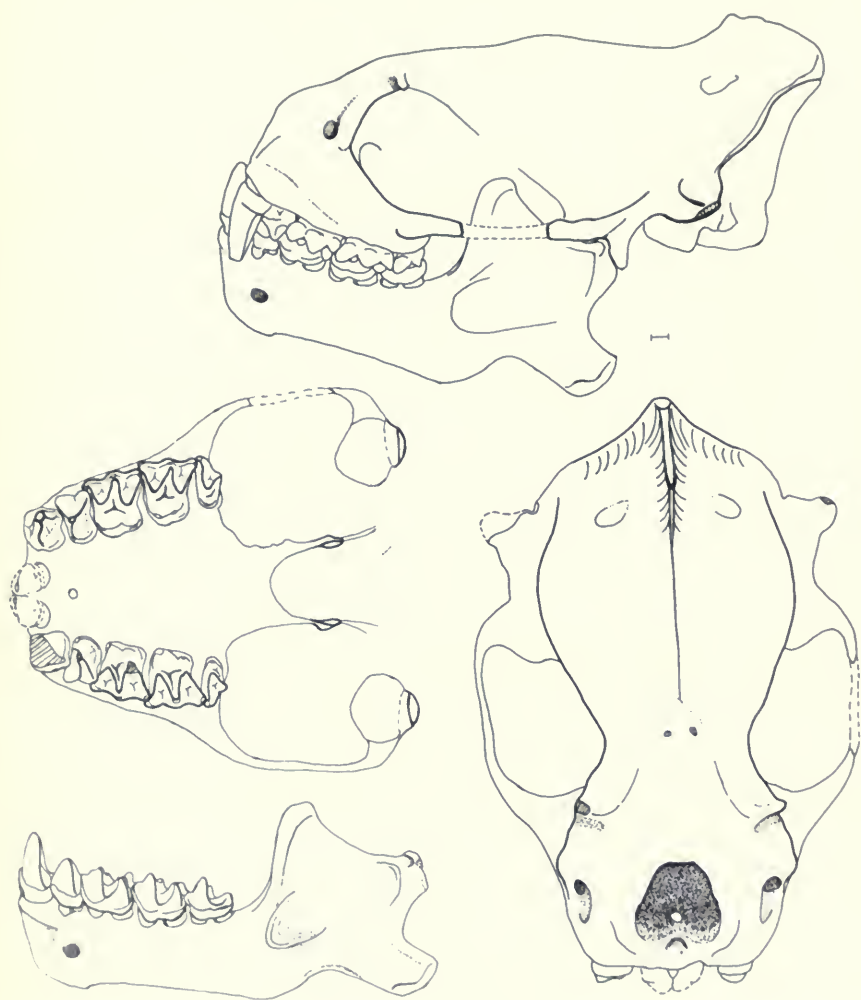
Cheiromeles parvidens ♂

FIG. 19. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible of one species of *Cheiromeles*.

Cheiromeles

At the extreme in the principal components plot in Figure 4A, *Cheiromeles* is in the most positive position. It is a genus which consists of two large species, *C. parvidens* and *C. torquatus*, and is found in Indonesia and the Philippines. These giant molossids are distinctive not only because of their size, but also because they are virtually hairless and are commonly called the naked bats or naked bull-dog bats. Species of *Cheiromeles* are the most extreme members of the Molossidae in shape as well as in size (fig. 2). They have the thickest jaws (mean relative dentary thickness is 16.0 per cent), widest face, and some of the broadest-tipped wings (mean relative length of second phalanx is 16.8 per cent) in the entire family. *Cheiromeles* is extreme in all other jaw proportions, and it has an extremely well-developed posterior sagittal crest. As a result the general appearance is one of extremely powerful jaws and strong, stocky skull (fig. 19). Like many of the other bats in this quadrate (particularly of the conglomerate) PM^3 is lost as is the posterior commissure on M^3, the lips are not wrinkled, the ears are widely separated, and the basisphenoid pits are nonexistent.

Cheiromeles parvidens and *C. torquatus* form the most compact pair of any two molossids in the size-in distance analysis (at 0.301) and in the correlation analysis (at 0.982). It is possible that true *torquatus* is not represented in my study, but Koopman (personal communication) questions whether these two large molossids are separate species anyway. In the size-out distance analysis the two specimens are separated by a distance of 0.278. Several other pairs of molossids with distances of less than 0.300 are suspected by me or other authors of being two members of the same species instead of two separate species.

Next nearest neighboring species to both species of *Cheiromeles*, size-in, is *Eumops underwoodi* and, size-out, *Molossops temminckii*. Next most highly correlated to *Cheiromeles parvidens* is *Cynomops brachymeles* and to *Cheiromeles torquatus* is *Eumops underwoodi* (table 7). Nearest generic neighbors to *Cheiromeles* are *Molossops* at 0.884 and *Cynomops* at 0.974, and the most distant genus is *Otomops* at 1.743 (table 8).

The specimen of *Cheiromeles torquatus* (female specimen, GSL is 29.6 mm) is slightly smaller than *C. parvidens* (male specimen, GSL is 30.6 mm), but both are closely similar in shape.[4] I know that the great development of the posterior sagittal crest allows a large area for temporal muscle origin, and although no food data are available, the bats should be easily capable of eating large, well-armored insects. I predict that *Cheiromeles* is rather slow flying for a molossid not only because of its relatively broad-tipped wings but also because of its great weight. Harrison & Medway (1959) reported that a specimen of *Cheiromeles torquatus* in Borneo weighed about 174 gm (*Eumops perotis*, the largest North American molossid, weighs only about 53.5 gm [Vaughan, 1966]).

Medway (1958) gave an excellent account of a colony of *Cheiromeles torquatus*, some 18,000 to 20,000 individuals, roosting in Niah Great Cave in western Borneo. Though the fecal pellets were not examined closely, only exoskeletal insect fragments were found. No bird remains were found, although Medway suspected that the large bat might be feeding on the small swiflet *Collocalia lowi* which nests in the same cave. Apparently wastes are eliminated both as feces and oral pellets. I recently examined fecal pellets taken from the floor of this cave

---

[4]Because *torquatus* is larger than *parvidens* (Miller & Hollister, 1921), I probably have two specimens of *parvidens*, leaving *torquatus* unrepresented here.

and found many recognizable parts of beetles and flying ants. Kitchener (1954a) reported that an individual *Cheiromeles* lived well in captivity on a diet of grasshoppers and moths.

Besides caves, *Cheiromeles* are known to live in small colonies in hollow Tapang trees (*Abauria*) (Harrison, 1954). Walker (1975) reported the large bat to have been found in rock crevices and in holes in the ground. I cannot find the source of this information, but if this heavy bat takes flight from the ground, it surely requires a tremendous amount of lift. Whether the longer phalanges of the digits and increased camber produces enough lift for *Cheiromeles* to take flight from the ground is certainly an interesting question.

An unusual adaptation in *Cheiromeles*, thought to be useful in climbing in hollow trees (Kitchener, 1954b), exists in the form of pouches under each wing which open toward the tail. These pouches are not for carrying young (usually twins) as was first thought but for the folded wing distal to the metacarpals. Only the forearm, adpressed metacarpals, and thumb protrude, enabling the bat to move agilely about.

Eumops

The final genus, and perhaps the most interesting, is the New World *Eumops*, a group almost as variable as the family itself. Seven species—*E. auripendulus, E. bonariensis, E. glaucinus, E. hansae, E. maurus, E. perotis,* and *E. underwoodi*— are represented in my study. They are medium to large molossids which range in GSL from 19.5 mm in *E. hansae* and *E. bonariensis* to 30.4 mm in *E. perotis* (fig. 20, table 1, appendix A).

Most variation occurs along axis II and positioning can be accounted for by the highly correlated jaw proportions, but on axes III and IV the positioning of the bats is merely an averaging of opposing and variably combined characters (fig. 4). Extremes on the jaw axis (II) are *E. perotis* with the thinnest dentary (relative thickness is 9.0 per cent) on the negative end and *E. auripendulus* with the thickest dentary (relative thickness is 14.0 per cent) on the positive end. This placement makes *perotis* much like the *Otomops-T. macrotis* extreme and *auripendulus* much like the *Molossus* extreme. Further, *auripendulus* has entirely lost the posterior commissure on M^3 and bears only a small PM^3, whereas *perotis* has not entirely lost the commissure and maintains a moderate-sized PM^3. The relatively small *hansae*, with medium dentary thickness and the most elevated jaw joint of the genus, has the most complete toothrow with full N-shape on M^3 and moderate PM^3. *Eumops maurus*, a slightly larger *Eumops* which is medium in all jaw proportions, has less than half the posterior commissure present on M^3 and has lost its premolar (however, specimens of *maurus* from Surinam have this tooth; Eger, 1977). The remaining three *Eumops* bear a small PM^3, slight commissure present on M^3, two with thin jaws (*bonariensis* and *glaucinus*), and the other, *underwoodi*, with jaws more like *auripendulus* (table 6, appendix A).

Axes III and IV are not highly correlated with the characters of the species of *Eumops*. Though several *Eumops* have large anteriorly directed ears, all except *hansae*, which has separated ears, are coded for having the intermediate condition of joining (specimens in fluid that I have recently examined show that at least *perotis* is miscoded—the ears appear to be well joined). All have moderate to deep basisphenoid pits and all have lips with the microscopic wrinkles (not deep ones). The wing tips are narrow (mean relative length of second phalanx is

6.6 per cent), and all but two have well-developed lateral lambdoidal crests (*hansae* and *bonariensis*).

In the multi-dimensional PCA plots (fig. 4), the smallest species of *Eumops*— *bonariensis* and *hansae*—are difficult to separate from *Tadarida*, *auripendulus* is difficult to separate from the *Molossus* swarm, and *maurus* and *glaucinus* are close to *Promops*. *Eumops underwoodi* and *perotis*, the two largest *Eumops*, are relatively isolated from any other group.

Size-out distance indicates that six species of *Eumops* are nearest neighbors of each other (table 7). *Eumops auripendulus* is nearest *Molossus bondae*, then *M. sinaloae*, and finally *E. glaucinus*. The average least distance within the genus (size-out) is 0.560, the most dispersed average in Table 5.

Size-in distance also places six of the seven *Eumops* nearest congeners. *Eumops bonariensis* is nearest *Chaerephon nigeriae* and several other species of *Chaerephon* or *Tadarida*. The closest congeneric neighbor of *bonariensis* is *maurus*. Average least distance, size-in, for the genus is 0.607, one of the largest averages in the table (5) and one which is affected largely by size variation in the species of *Eumops*.

Clustering by correlation again indicates six of seven species to be most highly correlated with congeners. *Eumops hansae* is most highly correlated with *Tadarida aurispinosa* and next most correlated with congener, *bonariensis*. Nearest generic neighbors of *Eumops* are *Neoplatymops* (0.782), *Chaerephon* (0.784), and *Promops* (0.818), and its farthest neighbor is *Cheiromeles* (1.404).

There are some interesting relationships of size and shape which occur in the jaw structure of several of the *Eumops* species. Regressions of jaw proportions on a size variable, GSL, show that *E. perotis* has uniquely thin jaws for a bat its size (fig. 7). *Eumops perotis* has well-developed jaw muscles and relatively large teeth (table 3). Besides *Cheiromeles*, *E. perotis* is one of the most extreme in molossid shapes.

With the kind of morphological variation present in the genus, food data from one species could not represent the genus as a whole. Species of *Eumops* seem to contain large and medium bats with thick dentaries and large and small bats with thin dentaries. Stomachs of six *underwoodi* (large with thick jaw) contained 47 per cent beetles, 6-10 mm in length; 31 per cent grasshoppers, 40-60 mm in length; 12 per cent leafhoppers; and 10 per cent Lepidoptera (Ross, 1967). Another stomach was found to contain four large (40 mm) June beetles (Melolonthinae) and two larger (60 mm) long-horned beetles (Cerambycidae). On the opposite extreme, *Eumops perotis* with thin jaws (sample size of nine) was found to have taken exclusively the abdomens of large hawk moths up to 60 mm long (Ross, 1967). Easterla & Whitaker (1972) reported that in 18 specimens 100 per cent contained 79.9 per cent Lepidoptera and 55.6 per cent contained 16.5 per cent Gryllidae and Tettigoniidae. Data support the prediction that a large molossid with thick jaws eats large, hard items such as beetles, and that a large molossid with thin jaws is taking and eating large soft-bodied prey such as moths.

Variation in the wing tips of species of *Eumops* is not as great as in the jaw structure. All have narrow wing tips, but there are few data on the flying habits of any of the species. Vaughan (1966) has assigned *E. perotis* the highest aspect ratio in his study of several species including three molossids and has calculated that its minimum flight speed is 14.7 m.p.h., also the highest figure in the

Eumops bonariensis ♂
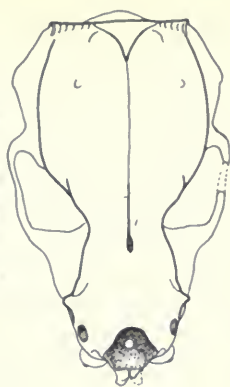
Eumops hansae ♂
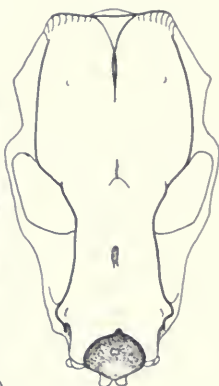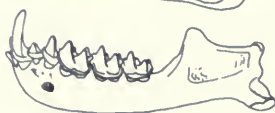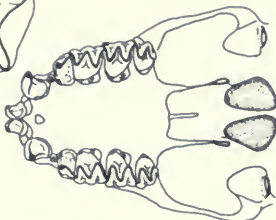
Eumops glaucinus ♂
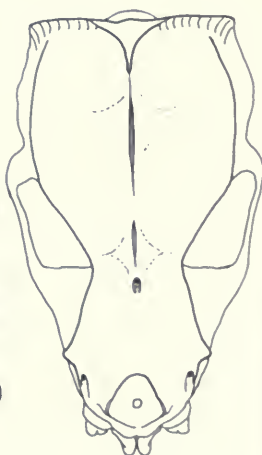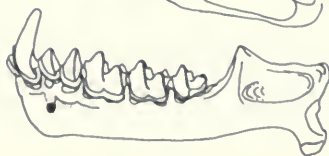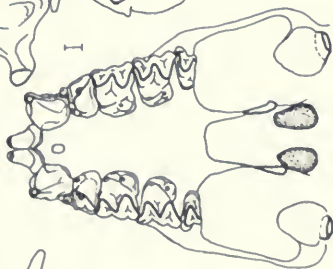
FIGURE 20.

90
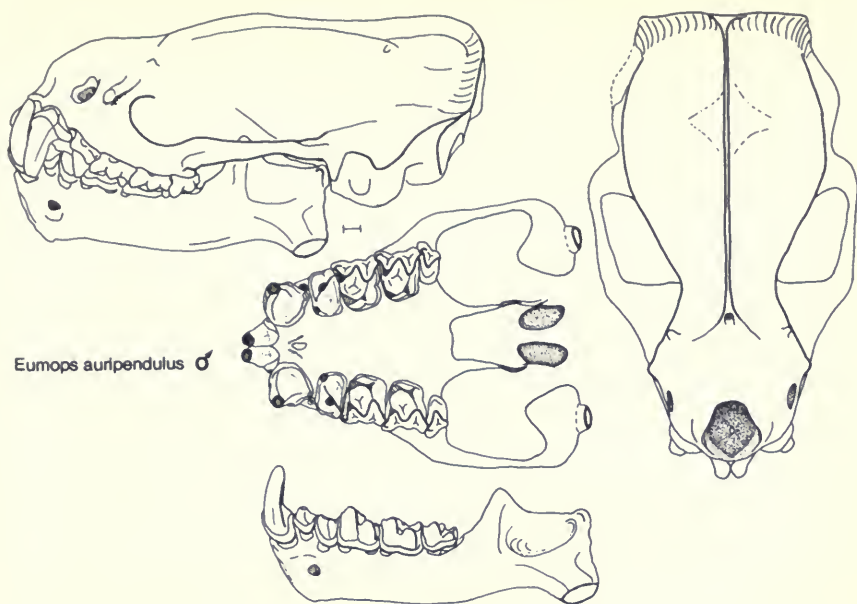
Eumops auripendulus ♂
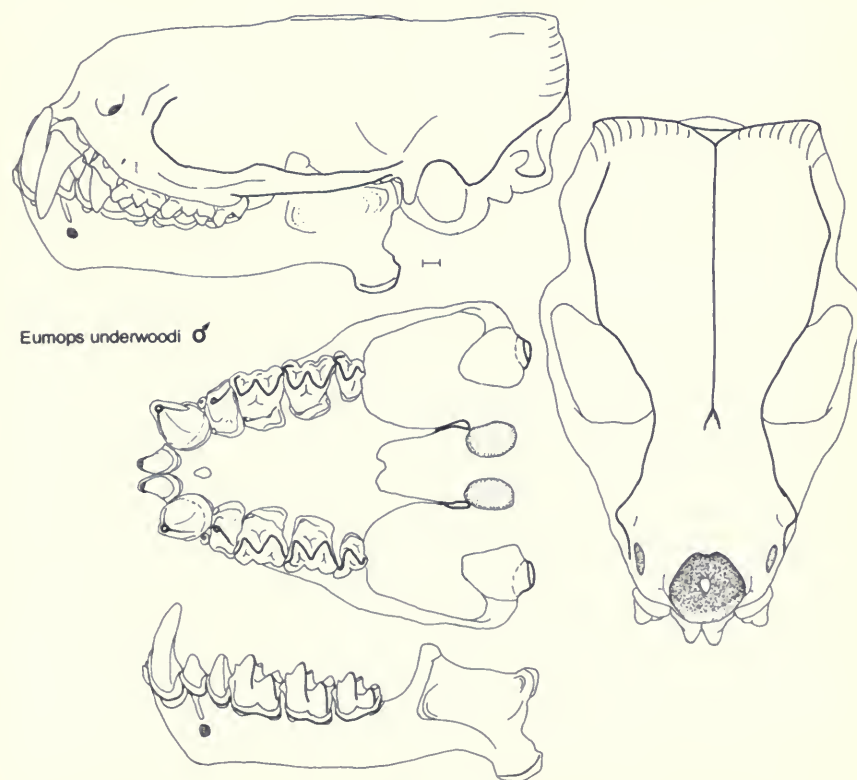
Eumops underwoodi ♂

FIGURE 20.

91
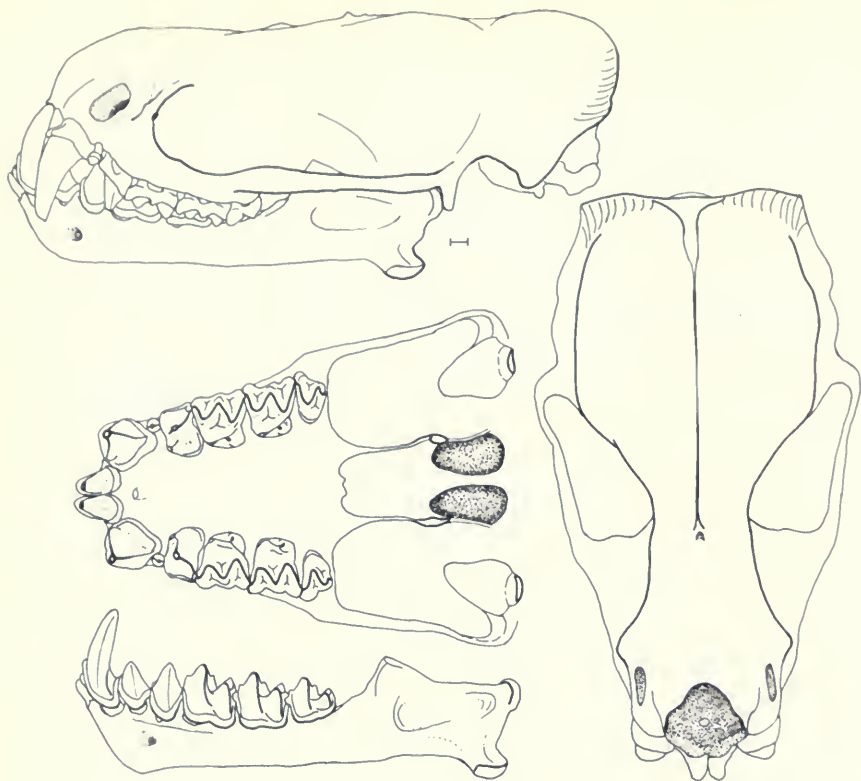
Eumops perotis ♂

FIG. 20. Six species of *Eumops* arranged from small to large. Lateral, dorsal, and occlusal views of the skull and lateral view of the mandible are given for each species.

study. These high figures make *E. perotis* the fastest flying bat in Vaughan's study. This large species of *Eumops* lives high in cliffs and is said to free-fall before it can fly. *Eumops underwoodi*, another large species, is thought to be much like *E. perotis* in that it lives in high, dry places. Findley et al. (1972) calculated the speed in *E. underwoodi* to be at least 27 m.p.h., but the authors thought this figure was an underestimate. *Eumops underwoodi* has also been found with *E. glaucinus* in tropical deciduous forest (Carter et al., 1966). LaVal (1969) reported that he took *E. glaucinus* over a shallow river surrounded by thorn forest and gallery forest. *Eumops auripendulus* has been found in belfries and roofs (Brosset & Dubost, 1967) and under loose bark (Jones, 1966), but where it flies has not been reported. Little is known about the smaller species of *Eumops* except for Fenton's (1972, p. 295) comment that *E. hansae*, as with several molossid species, is "caught only in the upper levels of the canopy." Marinkelle (1970) mentioned that a specimen of *E. bonariensis delticus* was taken in a net set in a rain forest on a river bank in southwest Colombia.

The loud noises emitted by *E. perotis* and *E. underwoodi* have been mentioned before. Whether the small species are as loud is not known. They do not all have ears as large as *E. perotis* nor do all live in dry places, leading me to suspect that their voices might be different.

Two species of vespertilionid bats, *Mimetillus* and *Nyctalus*, added to the analysis as being molossid-like have characteristics similar to *Mormopterus* but are more extreme on axis III (fig. 4, appendix A). The vespertilionids have wide faces and widely separated ears like species of *Mormopterus, Molossops, Cynomops,* and *Cheiromeles*. These two bats had to be coded in such a way as to fit into the trend of variation which occurs in molossids; hence, a coded character may not exactly describe (often an underestimate) the actual vespertilionid state and may cause these two bats to be more phenetically similar to molossids than they really are. For example, the degree of emargination of the anterior palate in the two vespertilionids is much greater than that in any species of molossid, but the two were only given the largest molossid code. Probably as a result of this underestimation, *Mimetillus* and *Nyctalus* do not appear as phenetically distinct from molossids as do the two species of *Cheiromeles* in my analysis.

ECOLOGY

What niches do molossids occupy? Is there competition for food and roost sites? How is coexistence possible? To answer these questions best, one would need to monitor the actual movements and behavior of molossids in their natural environment. Molossids, however, are difficult to capture, and because there are only a few specimens of many species, even the taxonomy of the group has not yet been adequately worked out. I think that some predictions about a molossid's ecological role can be made based on the morphology of the animal. Several authors have used this predictive method but usually with only a few morphological characters which represent trophic adaptations. Findley (1973, 1975) applied multivariate morphology to predict structure of several bat faunas. He used different distance measures and compared 1) how close, on the average, bats were to one another on different continents and in temperate or tropical regions and 2) how dispersed a fauna or community was in these places. Here, I describe the structure of three molossid bat faunas from a morphological viewpoint. At the end of the evolution section I compare the three faunas statistically and examine each for which might be the oldest fauna.

Molossids are unique among Chiroptera as the nocturnal counterparts of swifts because they are high, swift, and direct fliers (Fenton, 1975). In this habitat, probably few flying vertebrates are in intensive competition with molossids for food (although there may be more competition for shelter). Recently the subject of the ecological interaction between bats and nocturnal birds has been more fully investigated by Fenton & Fleming (1976). Chiropteran interfamilial competition for food or shelter is poorly known and outside the realm of my study. Here, I examine the family as an entity, different from other flying vertebrates, for geographical patterns in morphology and whether morphologically similar molossids are sympatric or allopatric. General ideas of intrafamilial competition among molossids are elucidated.

From the ecologically important characters that emerge from the principal components analysis, I can broadly represent the capabilities of the bats. The

authors of those papers which use few morphological traits for ecological predictions tend to use those which may show some relationship to the size, type, or consistency of prey taken, and to the size and type of shelter sought, or both. Schoener (1965, 1968) thought that sympatric congeners of birds and lizards avoid competition by concentrating on different-sized food items, whereas Tamsitt (1967), believed that the roosting site is more important in the composition of neotropical bat communities. Both McNab (1971) and Kock (1973) think that particle size of food and type or consistency of food are important parameters for successful coexistence of congeners.

Highly correlated characters from the PCA and ones I think are important in separating species of molossids in a fauna (and possibly a community) are general size (represented by GSL), which determines not only size of prey taken but also availability of roosting site; a jaw character (represented by relative dentary thickness), which determines whether hard or soft prey is taken; and a wing character (represented by relative length of the second phalanx of finger IV), which I think is related to maneuverability and speed of flight and, thus, how prey are taken or where a roost is located.

With these characters, the bats can be represented in a three-way morphological matrix, similar to the food niche matrix of McNab's (1971), where each geographic fauna is divided into cells to represent a molossid of a certain size and type (table 10). Geographic divisions correspond with the areas of concentrations of molossids: the most populated being the Ethiopian and Neotropical regions, and the least populated being the Eurasian and Australasian regions. Divisions in the size character and wing character occur at approximately 0.5 standard deviation unit from the mean and yield the categories SMALL-, MEDIUM-, and LARGE-sized bats and THIN-, MEDIUM-, and THICK-jawed bats (figs. 3, 21). I believe I can make predictions with some confidence as to habitat utilization for the small- and large-sized bats and thin- and thick-jawed bats but not for ones in the intermediate category. The wing character has a bimodal distribution, hence, the categories NARROW and BROAD wing tips. Although small, medium, and large sizes of molossids are marked off, increases of 1 mm in GSL remain in the matrix for ease of explanation. It is also possible that increments in size of this degree may be ecologically important in bats.

Taxonomically the Ethiopian and Neotropical regions have a similar composition: each has two large genera, several smaller genera, and two genera are shared. The greatest concentration of species of *Mops* and *Chaerephon* occurs in Africa. No representatives of these genera are found in the New World and only five occur in the Indo-Australian region. Similar concentrations occur in the Neotropics in species of the genera *Eumops* and *Molossus*, both of which are endemic. The smaller endemic genera are *Platymops*, *Sauromys*, and *Myopterus* in the Ethiopian region; and *Neoplatymops*, *Molossops*, *Cynomops*, and *Promops* in the Neotropics. *Otomops* is confined to both Old World areas, and *Tadarida* and *Mormopterus* are found in both the New and Old Worlds.

In general body size, medium-sized molossids compose over 50 per cent of the molossid fauna in all three geographical regions (table 10). In the two regions of highest concentration of molossid species, the Ethiopian has a greater percentage of large bats than does the Neotropical (28 per cent versus 17 per cent); while the Neotropical region has a greater percentage of small bats than does the Ethiopian (28 per cent versus 17 per cent). Bats in the Indo-Australian region follow the pattern found in the Ethiopian.

TABLE 10. Morphological niche matrix for molossid faunas based on three morphological characters: greatest skull length, jaw thickness, and wing tip width.

GSL (mm.)	ETH Thin Narrow	ETH Thin Broad	ETH Medium Narrow	ETH Medium Broad	ETH Thick Narrow	ETH Thick Broad	NEO Thin Narrow	NEO Thin Broad	NEO Medium Narrow	NEO Medium Broad	NEO Thick Narrow	NEO Thick Broad	IA Thin Narrow	IA Thin Broad	IA Medium Narrow	IA Medium Broad	IA Thick Narrow	IA Thick Broad
13.0 (small)										TR MINUA MP TEMMA NEOPLATA								
14.0		TR ACETA				XIPHONYC												
15.0		TM NANUA PLATYKUA						TR KALIN	TR PHRUD CP PLANA		M COIBEA			TR PLANA		TR LORIA		
16.0		TC CHAPI				TR JUGUA		T BRASIA								TR NORFA		
17.0 (medium)		SAUROMYS MYOP NHA		TC MAJOR TC PUMIA TC BENMI TM LEONA					CP GREEA PRO NASU		M MOLOSS M BONDAA							TR BECCR
18.0		T ANSORA TC MIGIA TC RUSSA				TM BRACH TM THERA	T LATICA				M TRINIT							TM SARSA
19.0		T AEGYPA		TC BIVIA			T FENORA E BONARA		E HANSAA		M SINALA			TC JOHOR OTO PAPU		TC PLICA		
20.0						TM DEMOA TM CONDA			T AURISA E MAURUS PRO CENA		CP BRACA M PRETIA							
21.0		TC ALOYA				TM NIVEI					M ATERA			OTO SECA		T KUBORI		TC JOBEN TM HOPSA
22.0 (large)			T FULAIN	T LOBATA														
23.0				TM TREVO		TM NIANG MYOP ALB	T MACROA		E GLAUCA		E AURIPA			T AUSTRA				
24.0			T AFRICA			TM CONGA								T TENIQA OTO WROA				
25.0																		
26.0									E UNDERA									
27.0		OTO MARA				TM MIDAA	E PEROTA											
28.0																		
29.0																		
30.0																		C TORQUT C PARVID

ETHIOPIAN REGION · NEOTROPICAL REGION · INDO-AUSTRALIAN REGION

95

FIG. 21. Distributions of the jaw (DTHIC DL) and wing (4M 2PHAL/DIGIT 4) characters. The jaw character is divided at approximately 0.5 standard deviation units from the mean to make the categories THIN, MEDIUM, and THICK. The wing character is bimodal and divided into the categories NARROW and BROAD.

The similarity in faunas of molossids with thick and thin jaws is striking. Species of *Molossus* from the Neotropics (fig. 9) and species of *Mops* from Africa (fig. 11) represent two kinds of bats with thick jaws and well-developed sagittal crests. I think these two genera can be thought of as ecological counterparts, and both are probably consuming hard-shelled prey. A similar example can be drawn for bats with thin jaws: *Otomops martiensseni* in Africa (fig. 13) and *Tadarida macrotis* (fig. 15) in southwestern United States are both probably eating soft-shelled prey. Though both New and Old Worlds have a similar percentage of bats with thick jaws, the Old World has more bats with thin jaws. It would be interesting to know if there is a greater number of soft-bodied prey available to molossids in the Old World. Further interesting questions can be asked of the bats with thick jaws. In both the Neotropics and Africa a graduated size series of thick-jawed species occurs: Do these bats specialize on hard prey as neatly graduated in size as themselves? How big a difference in general size has to occur to allow coexistence with other similarly built molossids? On the whole, the Ethiopian fauna contains a greater variety of molossids because not only does this fauna have very small bats of both jaw extremes but also very large bats of both jaw extremes. The Neotropical fauna does not have a very large bat with thick jaws, nor does the Indo-Australian fauna have a very large bat with thin jaws.

The wing character (fig. 21) has a bimodal frequency distribution. Most of the bats with narrow wing tips are in the New World, whereas most of the bats with broad tips occur in the Old World. Two of the large African *Tadarida* (*T. africana* and *T. fulminans*) have wing tips similar (though not quite as narrow) to those of New World bats, especially species of *Eumops*. There is evidence that these two *Tadarida* roost in cliffs as do several species of *Eumops*. Similarity in the skulls of *T. africana* and *E. glaucinus*, bats of similar size, are shown in Figures 14 and 20. Possibly the two *Tadarida* are ecological vicars with some of the species of *Eumops*. Randolph Peterson (personal communication) suggested that *T. lobata*, another similar, large African species, is especially *Eumops*-like because of its long, narrow rostrum. One last pair of ecological (if not phylogenetic) counterparts exist with species of *Myopterus* in Africa and *Cynomops* in the Neotropics (figs. 18, 17).

Only five New World species possess broad wing tips, and all are small species: *T. brasiliensis*, two species of *Mormopterus*, and two monotypic genera, *Molossops* and *Neoplatymops*. Most of the 17 small molossid species in the world have broad wing tips. In the New World, however, there are exceptions: a species of *Molossus*, a species of *Cynomops*, and a species of *Mormopterus*, all three of which have narrow wing tips.

The remaining New World *Tadarida* (the *T. macrotis* group), *Eumops*, *Molossus*, and *Promops*, possess extremely narrow wing tips. What is it about the New World environment that selects for narrow-tipped wings in molossids? Are ancestors of these bats ones which may have migrated from the Old World? Although the last is an intriguing question, the bats that today appear to be most closely related to Old World forms, *Tadarida brasiliensis* and one or two species of *Mormopterus*, are bats with relatively broad wing tips. Also, the long-distance yearly migrations which occur in the New World are undertaken by both *T. brasiliensis* and *T. macrotis*.

Simplified faunal pictures such as the matrix in Table 10 are interesting, but are they helpful when realistically looking at a community of sympatric species?

Though the known geographical ranges of molossids are far from accurate, I think even the most general prediction of possible intrafamilial competition adds to the knowledge that now exists for molossid species.

Overlap in the morphological cells in the matrix means that the bats involved are approximately the same size, fly in a similar way, and feed on the same types of insect prey. In cells of overlap it would be helpful to know whether the molossids are allopatric, sympatric, or syntopic. Allopatry is not very interesting to the present coexistence of species, although it may represent a result of earlier competition or isolation. It is the sympatric situations that require close examination. Field data to clarify whether the sympatric species are actually syntopic are not always at hand. In any case it may be instructive to see if the overlapping species are also nearest phenetic neighbors in the 76-character space described in the first section.

Two overlapping, small Ethiopian molossids with broad wings and thin jaws, *Mops nanula* and *Platymops*, are mostly allopatric. The first is a western forest species (Rosevear, 1965); whereas the second, an eastern species, lives in narrow crevices in dry, open areas (Hayward, personal communication). There may be some geographical overlap in western Kenya where *M. nanula* has been found in light, riverine forest in dry, grassy *Acacia* country (Start, 1969). *Platymops* is one of the flat-headed molossids and lives in very narrow crevices.

The medium-sized *Sauromys petrophilus* and *Myopterus whitleyi* are also separated geographically and ecologically. *Sauromys*, another flat-headed molossid, is a southern African dry country species (Irwin & Donnelly, 1962); whereas *Myopterus whitleyi* is a western and central forest species.

Three overlapping medium-sized species with broad wings and thin jaws are *Tadarida ansorgei*, *Chaerephon nigeriae*, and *C. russata*. These three are near neighbors morphologically (see table 7), and are all found in Zaire. That they are actually syntopic is not known. *Tadarida ansorgei* is a savannah species and prefers to roost in rocks (Allen et al., 1917; Verschuren, 1957), whereas *Chaerephon nigeriae* is a species of the Guinea woodland, also savannah country, but roosts in trees or houses (=*cistura* of Allen et al., 1917; Koopman, 1965). Fenton & Peterson (1972) reported *russata* to be consistently associated with the edge of "invasive Guinea woodland" near "high forest" (terms after Rosevear, 1965). Seemingly these three species have slightly different niches, even if they were to be syntopic.

Another cell having overlap occurs with four species of medium-sized bats with broad wings and medium-thick jaws: *Chaerephon bemmelini*, *C. major*, *C. pumila*, and *Mops leonis*. The species of *Chaerephon* are near neighbors of one another (table 7) but not of the species of *Mops*. *Mops leonis* is a high forest species which roosts in trees and under roofs (Rosevear, 1965). Though all three species of *Chaerephon* are inhabitants of Zaire, they have not been found at the same locality. *Chaerephon bemmelini* is thought to be associated with mixed forest rather than dense high forest or open savannahs (Peterson, 1971b), whereas *C. major* is more of an inhabitant of the savannah (Verschuren, 1957; Hayman & Hill, 1971). Both species are known to roost in rocks. *Chaerephon pumila* has been reported from dense gallery forest (Verschuren, 1957) and from open woodland (Rosevear, 1965). It is a common and widespread bat which roosts in tree holes and houses. These four, if syntopic, would be interesting to study to see how their coexistence is possible.

Two medium-sized, broad-winged bats with thick jaws, *Mops brachyptera* and *M. thersites*, are thought to be either allopatric, closely related forms or subspecies of one another (Koopman, 1975). *Mops thersites* is the western form and found in the high-forest zone (Rosevear, 1965); but *M. brachyptera*, the eastern form, is very poorly known.

Mops demonstrator and *Mops condylura* are not only the same size with similarly shaped wings and jaws, but they are also syntopic. Both have been found in the Garamba National Park in Zaire, both roost in the tree, *Vitex doniana*, and both live in apparently the same savannah habitat (Verschuren, 1957). However, the two are never found together in the same roost but maintain monospecific groups. *Mops condylura* is one of the most common molossids and one that also inhabits man-made habitations. Verschuren noted that although the two animals when alive are very similar to one another, *M. demonstrator* (*faradjius* in his report) is not as clumsy or heavy in appearance as *M. condylura*. The two are nearest phenetic neighbors.

The last overlap consists of *Mops niangarae* and *Myopterus albatus*, both large bats with broad wings and thick jaws. Both were found near Niangara in northeastern Zaire by Lang & Chapin (1917), and both were listed as being found in rain forest or extensive gallery forest (Allen et al., 1917). Hayman & Hill (1971), however, reported that *Myopterus albatus*, in contrast to *Myopterus whitleyi*, "seems to be an inhabitant of the savannahs." Lang & Chapin had remarked, too, that they thought *Mops niangarae* should also be found in more open country. Where these two large species actually live and how they coexist is simply not known. Although *niangarae* is the nearest neighbor to *albatus*, the size-in distance is great (0.757, table 7), and the two are not nearest neighbors in the size-out analysis. The two are not alike phenetically and probably have different ecological requirements.

A more obvious question may be asked while looking at the morphological niche matrix: Do molossids that we know are sympatric overlap on the matrix? Two early studies which involve all the Chiroptera in an area have been most useful for examination of sympatric species of molossids. Allen et al. (1917) listed which bats were collected at each of their localities (area of 30- to 40-mile radius from the locality) in northeastern Zaire. I think molossids collected at one place can be thought of as sympatric species, though not necessarily as syntopic ones.

At Faradje, *Tadarida ansorgei*, *Chaerephon chapini*, *C. major*, *Mops demonstrator*, *M. trevori*, and *M. midas* were captured. None of these overlap in the matrix (table 10). At Medje, *C. russata*, *M. leonis*, *M. condylura*, and *M. congica* were found; and none of these overlap in the matrix. At Niangara, *C. nigeriae* (originally called *cistura*, see Koopman, 1965), *M. nanula*, *M. niangarae*, and *Myopterus* overlap but probably are not syntopic. In general, the matrix is a fairly good ecological separator of molossids, as each of these sympatric bats has a cell (and by inference, ecological niche) to itself.

Verschuren (1957) studied the ecology of bats in Garamba National Park, an area of 480,000 hectares, in northeastern Zaire. I also consider molossids found here sympatric: *T. ansorgei*, *C. pumila* (including *limbata*), *C. major*, *M. condylura*, *M. demonstrator*, *M. midas*, *M. trevori*, and *Otomops martiensseni*. Hayman & Hill (1971) reported the later collection of *C. nigeriae* from this park. Several overlaps occur, but these can be explained. *Tadarida ansorgei* and

Chaerephon nigeriae are not found in the same locality in the park, and though both occur in the savannah habitat, they prefer different roosts. *Chaerephon pumila* and *C. major* are also found at different localities in the park, but even so, *pumila* seems to prefer the forest and *major*, the savannah. Though similar in habits and habitat as mentioned earlier, *Mops condylura* and *M. demonstrator* never occur together in the same roost. *Mops condylura* also makes use of houses for roosting but *M. demonstrator* does not. These two are probably closely related sibling species and are coexisting as a result of man's activities.

Verschuren reported several occurrences of groups composed of two species. One contained 150 *M. condylura* and one *M. trevori*, another contained equal small numbers of *C. major* and *T. ansorgei*, and a third small group contained *M. demonstrator* as the dominant and *M. midas* as the subordinate. Neither member of these pairs overlap on the matrix. One is either larger or of different wing or jaw shape than the other or has a combination of differences in the three characteristics.

Four overlaps occur in the Indo-Australian matrix, but the species of each overlapping pair seem to be allopatric (table 10). Few specimens and fewer field data are available for the species in this region. There is doubt as to whether some of the taxa are really specifically distinct. The three small species of *Mormopterus* are probably confused taxonomically (McKean & Price, 1967), and there is some doubt as to whether *Cheiromeles* contains two species or one (Koopman, personal communication). Until more specimens and data are available, little more can be said about this situation.

Neotropical molossids also overlap in several places on the morphological niche matrix. Unfortunately, fewer field data are available concerning the actual ecology of these bats. A study such as that of Verschuren (1957) has not been completed. Three small bats with medium-thick jaws and broad wing tips are *Mormopterus minutus*, *Molossops temminckii*, and *Neoplatymops mattogrossensis* and overlap on the matrix. *Mormopterus minutus* from Cuba is allopatric with the other two species which are probably sympatric in eastern South America. *Molossops* has been found in a decaying log, possibly indicating a mesic place, and *Neoplatymops* has been found in a xeric place under a slab of rock in a savannah (Peterson, 1965). The latter is the only New World flat-headed molossid.

Data on the remaining overlaps in Table 10 for New World molossids are spotty and are listed with few or no comments. Two pair appear to be allopatric: *Mormopterus phrudus* from Peru and *Cynomops planirostris* from central and eastern South America; and *Tadarida femorosacca* from western and central Mexico and southwestern United States and *Eumops bonariensis* from southern Mexico and south into South America. Two other pair seem to be allopatric for most of their distribution but may be sympatric in a small portion of it. *Cynomops brachymeles* from much of South America and *Molossus pretiosus* from Mexico, Central America, and Colombia have both been found in Venezuela. *Cynomops greenhalli* from Mexico, Central America, and Colombia and *Promops nasutus* from Paraguay, Brasil, and Venezuela have both been found on Trinidad. Only two pair remain which are sympatric through most of their distribution. *Molossus bondae* and *Molossus molossus* are found in most of Central America, Colombia, and Venezuela. No data exist suggesting factors which may allow coexistence of these two very similar bats. *Tadarida aurispinosa* and *Promops centralis* are allopatric with *Eumops maurus*, but the two are sympatric with each other in

western Mexico and probably in South America. Whether the two are syntopic is unknown.

McNab (1971) reported that tropical molossid faunas on a number of smaller islands in the Caribbean are made up of similar kinds of bats. He noted that in several cases at least a small species of *Molossus* and a small species of *Tadarida* are found together and that "there must be some important ecological segregation of those bats such as the level or area at which feeding occurs." From the matrix and from food data presented in the first section, I expect that because of the different dentary configurations, the species of *Tadarida* may well be concentrating on small, soft prey and the species of *Molossus*, on small, hard prey.

I suggest in the preceding discussion that there are few instances of morphologically overlapping sympatric molossids in the Neotropics and none in the Indo-Australian region compared to the Ethiopian fauna. Perhaps this means that molossids in the Neotropical and Indo-Australian faunas presently suffer less from intrafamilial competition than molossids in the Ethiopian fauna.

EVOLUTIONARY RELATIONSHIPS

Are molossids which are phenetically similar also closely related phylogenetically, or are they similar because they share an overall convergence of characters? Few data exist on ancestors of molossids, data which might have aided this discussion. Smith (1976) recently reviewed the known fossil Chiroptera, and Slaughter (1970) summarized the evolutionary trends of chiropteran dentitions. Because evidence from fossils is scanty, I feel justified in using the multivariate shape analyses coupled with several evolutionary theories to determine phylogenetic relationships among species in the family Molossidae. In this section, I discuss the overall phenetic groupings of molossids as summarized by the phenogram of the size-out distance matrix and decide what species form what I think are the natural genera based on similarity of shape. Additionally, I point out several characters that can be graded as to their primitive and derived nature in order to evaluate the phylogenetic relationships in the family. Although this is primarily a phenetic study, I present some idea as to which are the primitive and derived genera in the family. A final question is how have molossids radiated through time, and what is the geographic distribution of primitive and derived forms of molossids.

Two clustering methods concerned with shape relationships are the size-out distance analysis and the correlation analysis (table 7). Not only does the size-out distance analysis appear less affected by general size difference among the bats than does correlation, but also the phenogram from the size-out matrix has a higher co-phenetic correlation coefficient than does the correlation phenogram (0.754 versus 0.678). This coefficient indicates how well the phenogram represents the matrix from which it is taken; and though one is higher than the other, both indicate a level of representation of their respective matrices used by other authors (Schnell, 1970; Findley, 1972). The size-out analysis and phenogram are the basis for the following discussion, but evidence from the correlation analysis is included to enhance understanding of the shape relationships. A summary of each bat's nearest neighbor or most highly correlated neighbor is presented in Table 7.

Across the size-out phenogram in Figure 22, I have drawn two solid lines at
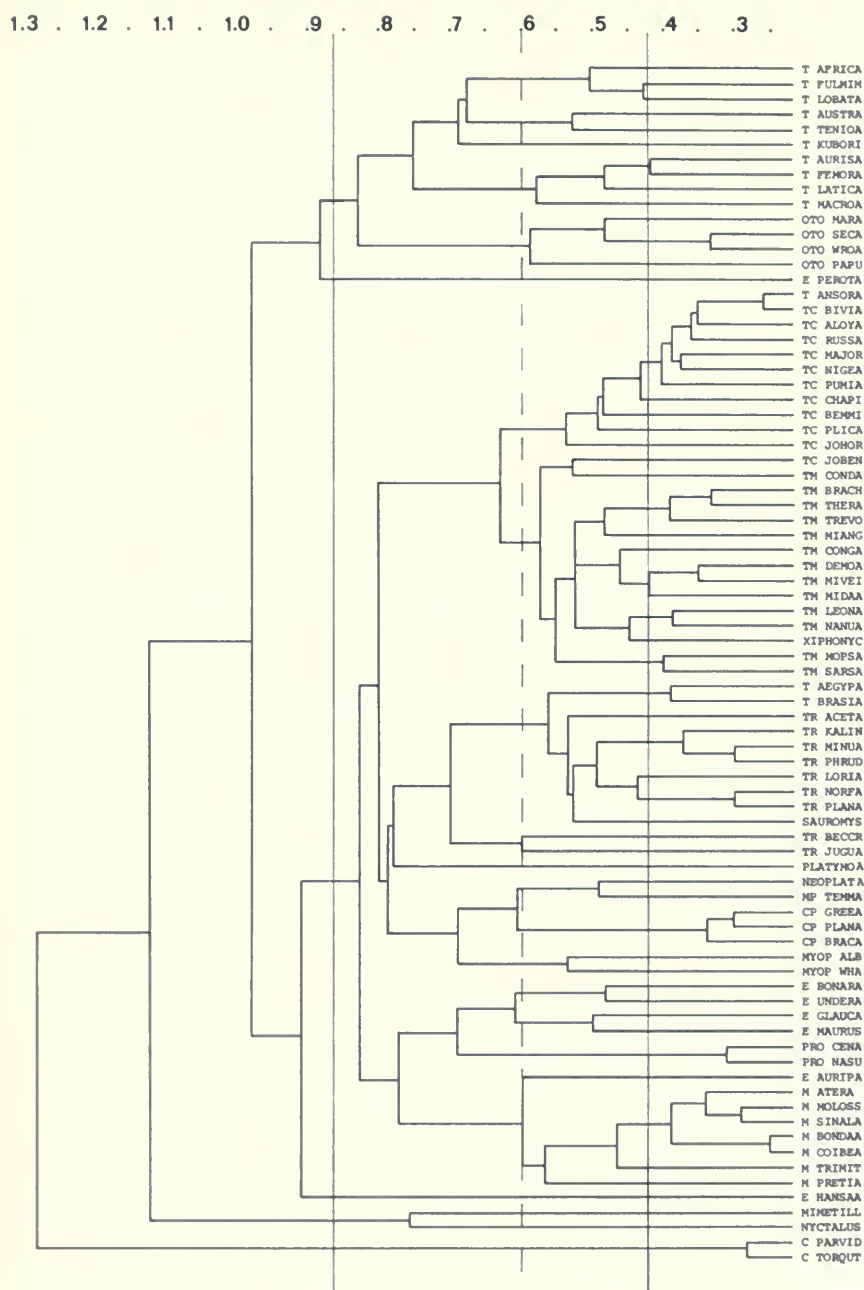
FIG. 22. Phenogram of molossids taken from the size-out distance matrix. Solid lines at 0.420 and 0.870 are the means of least and average distances, respectively, of the matrix. The dashed line at 0.600 is the line used to delineate 12 molossid genera of similar dispersion.

0.420 and at 0.870. The first is the average nearest-neighbor-distance computed from the distance matrix from which the phenogram was taken, and the second is the average value of all the elements of that matrix. Several genera are more tightly packed than others and the two lines are good indicators of the relative dispersion in each molossid genus. A third of the junctures occur at the level of the first line and 90 per cent, at the level of the second. The dashed line at 0.600 is the line I use to delineate 12 molossid genera of similar morphological dispersion. Seventy-five per cent of the junctures occur by the level of this line. The phenogram is most accurate at representing the data at the smaller distances where the bats are most alike and few averages have been taken, but is not as good at representing the greater, intergroup distances, where averages of averages occur.

In addition to the basic phenetic arrangement of the species, I use several ideas about evolution to help me interpret the relationships among the species. The first concerns the use of primitive and derived characters. Only a few of the 76 characters are conducive to this use because most of the quantitative characters cannot be classed as primitive or derived either because of size or functional morphology. The characters remaining are the multistate codes which I feel have some phyletic use when compared to the Vespertilionidae, a family of bats thought to be more primitive than molossids (table 11). No basisphenoid pits, widely separated ears (usually short and erect or perky), no wrinkles on the lips, a deeply emarginated anterior palate, a long second phalanx of digit IV, and 32 teeth are primitive states for molossids. The primitive tooth formula is $\frac{1}{3}\frac{1}{1}\frac{2}{2}\frac{3}{3} = 32$ where the I_3 and the PM^3 are well-developed, M^1 with distinct metaconule, and M^3 with a complete N-shaped cusp pattern (premetacrista present). Deep basisphenoid pits, well-joined ears over the nose (usually large and slouched or bonneted), finely wrinkled lips, no anterior emargination of the palate, short phalanx on digit IV, and 26 teeth are derived conditions. The derived formula is $\frac{1}{1}\frac{1}{1}\frac{1}{2}\frac{3}{3} = 26$ with PM_3 vestigial, M^1 without metaconule, and M^3 with premetacrista absent.

Because of the small sample size for each species and the subjectivity of the coded characters, I cannot discuss each slight change in each code for each species. The dental characteristics, because they are easier to determine (although toothwear is occasionally a problem), are given slightly more attention, especially if corroborated by other traits. In the section on generic considerations that follows, I summarize the specific relationships by examining the phyletic relationships (both phenetically and cladistically) among the genera.

The second and third ideas about evolution more or less help me define what a genus is within the Molossidae. My thoughts coincide with those of Maglio (1973, p. 14) who said, "All members of a genus share a fundamental adaptive zone different in some particular way from that of other such groups. This adaptive zone may or may not be precisely definable, but is inferred by the common possession of a particular suite of functionally integrated characters." More specifically, a genus tends to be made up of several animals of different sizes but with one basic shape, and the very large species are often allometrically much distorted compared to that basic shape. Probably evolutionarily, the easiest change to make is in size, not in shape. Schoener (1965, 1968) mentioned that, ecologically, species are more likely to expand first on a food axis of items of different size rather than a habitat axis. I assume the first axis has to do with size and the second with shape. Simpson (1944, p. 92) gave

TABLE 11. Primitive-derived traits for all molossid species, arranged in the same order as those in the phenogram (fig. 22); character states of seven of the traits are in Materials and Methods section. Within each column, the primitive state is on the left and the derived on the right, and the position of each number in the column visually reflects this. Broad (B) and narrow (N) wing tips are determined in the Ecology section (fig. 21), and actual number of lower incisors is given.

	EAR 123	PITS 12345	PALATE 54321	WRINKLES 1234	WING BN	INCISORS 642	PM^3 4321	M^1 321	M^3 123456
T AUSTRA	2	1[a]	4	3	B	4	2	3	1
T TENIOA	2	3	4	2	B	6	4	3	1
T AFRICA	2	4	4	4	N	4	2	2	3
T FULMIN	2	3	4	4	N	4	4	2	3
T LOBATA	2	3	4	4	N	4	4	1	3
T KUBORI	2	1[a]	4	3	B	4	4	2	1
T AURISA	3	3	3	2	N	4	4	3	1
T FEMORA	2	2	3	2	N	4	4	3	1
T LATICA	3	2	3	3	N	4	3	3	1
T MACROA	3	4	3	2	N	4	4	3	1
OTO MARA	3	5	3	4	B	4	4	1	1
OTO SECA	3	5	3	4	B	4	4	1	1
OTO WROA	3	5	3	4	B	4	4	1	1
OTO PAPU	3	5	3	4	B	4	4	1	1
E PEROTA	2[b]	4	1	4	N	4	3	2	4
T ANSORA	3	3	3	2	B	4	3	2	3
TC BIVIA	3	3	3	3	B	4	3	2	3
TC ALOYA	3	4	2	3	B	4	3	3	3
TC MAJOR	2	2	2	2	B	4	3	2	3
TC NIGEA	3	3	2	3	B	4	3	2	3
TC PUMIA	3	3	2	3	B	4	2	2	3
TC CHAPI	3	3	2	2	B	4	3	2	3
TC RUSSA	3	3	2	3	B	4	3	2	3
TC BEMMI	3	2	3	2	B	4	4	2	2
TC PLICA	3	3	2	3	B	4	4	2	2
TC JOHOR	3	3	2	3	B	4	3	1	2
TC JOBEN	3	3	2	2	B	4	3	1	2
TM CONDA	3	2	2	3	B	4	2	2	4
TM BRACH	3	3	4	2	B	4	3	2	4
TM THERA	3	3	3	2	B	4	3	2	4
TM TREVO	3	4	2	3	B	4	3	1	4
TM NIANG	1	4	2	3	B	4	3	1	4
TM CONGA	3	4	2	3	B	4	2	2	5
TM DEMOA	3	4	2	2	B	4	2	2	5
TM NIVEA	3	3	2	2	B	4	2	1	5
TM MIDAA	3	3	2	2	B	4	2	2	5
TM LEONA	3	2	3	2	B	4	3	2	5
TM NANUA	3	2	3	2	B	4	3	2	5
XIPHONYC	3	2	3	2	B	2[c]	4	1	5
TM MOPSA	3	3	3	2	B	4	1	2	6
TM SARSA	3	3	2	3	B	4	1	2	6
T AEGYPA	1	3	4	2	B	4	3	3	2
T BRASIA	1	2	4	2	B	6[c]	2	3	1

Table 11. *Continued.*

	EAR 123	PITS 12345	PALATE 54321	WRINKLES 1234	WING BN	INCISORS 642	PM^3 4321	M^1 321	M^3 123456
TR ACETA	1	2	4	3	B	6	1	2	1
TR KALIN	1	1	4	1	B	4	1	3	1
TR MINUA	1	2	3	1	B	4	1	2	1
TR PHRUD	1	2	3	1	N	4	1	3	1
TR LORIA	1	2	4	1	B	4	2	1	2
TR NORFA	1	2	4	1	B	4	2	3	1
TR PLANA	1	2	4	2	B	4	3	3	2
SAUROMYS	2	2	4	1	B	4	2	3	2
TR BECCR	1	2	4	2	B	4	1	3	1
TR JUGUA	1	2	4	1	B	6	2	3	1
PLATYMOA	1	1	3	3[d]	B	4	1	3	2
NEOPLATA	1	2	1	2	B	4	2	1	2
MP TEMMA	1	1	1	1	B	2	1	1	4
CP GREEA	1	1	1	1	N	4[c]	1	1	5
CP PLANA	1	1	1	1	N	4	1	1	5
CP BRACA	1	1	1	1	N	4	1	1	5
MYOP ALB	1	5	1	1	B	2	1	1	5
MYOP WHA	1	4	1	1	B	2	1	1	5
E BONARA	2	4	1	4	N	4	2	2	3
E UNDERA	2	3	1	4	N	4	2	1	4
E GLAUCA	2	4	1	4	N	4	2	2	4
E MAURUS	2	3	1	4	N	4	1[c]	2	4
PRO CENA	2	3	1	1	N	4	2	1	5
PRO NASU	2	3	1	1	N	4	2	1	5
E AURIPA	2	4	1	4	N	4	2	1	5
M ATERA	2	3	1	1	N	2	1	1	6
M MOLOSS	2	3	1	1	N	2	1	1	6
M SINALA	2	3	1	1	N	2	1	1	6
M BONDAA	2	3	1	1	N	2	1	1	6
M COIBEA	2	3	1	1	N	2	1	1	6
M TRINIT	2	3	1	1	N	2	1	1	6
M PRETIA	2	3	1	1	N	2	1	1	6
E HANSAA	1	5	1	4	N	4	2	3	1
MIMETILL	1	1	5	1	N	4	1	3	1
NYCTALUS	1	3	5	1	N	4	3	1	1
C PARVID	1	1	1	1	B	2	1	1	5
C TORQUT	1	1	1	1	B	2	1	1	5

[a]Long, shallow grooves instead of pits.
[b]Miscoded; ears are definitely joined with a band over the nose.
[c]Variable number of lower incisors.
[d]Difficult to code because upper lip is covered with thick hairs or spines.

an example from fossil-browsing horses which expand on a size basis before shifting into a grazing mode of existence.

Third, the notion of Cope's Rule, as elucidated by Stanley (1973), is that it may be easier for animals to radiate from a small than from a large relative body size, and that very large animals mark the end of some line of radiation. Thus, in each group discussed, I examine the large and small members of the group as well as which of the animals have primitive or derived characteristics.

Specific Considerations

The uppermost part of the phenogram is occupied by *Tadarida* from the Old and New Worlds, *Otomops*, and *Eumops perotis* (fig. 22). Bats of this assemblage are all located on the far negative end of axis II of the PCA (fig. 4), meaning they have thin jaws and probably eat moths and other insects with soft bodies. To show the similarities in the general form of four of the largest bats, drawings of their skulls are shown in Figures 13-15 and 20.

The first six OTU's (fig. 22) are species of *Tadarida* from the Old World and bats of more or less large size (GSL = 21.0 to 24.0 mm). All have some kind of basisphenoid depression (although *australis* and *kuboriensis* were not coded as such because their "pits" are atypically long with indistinct margins, fig. 14), joined ears, wrinkled lips, and emarginated anterior palate. *Tadarida teniotis*, with its well-developed I_3, has the most primitive tooth configuration of any molossid. All six bats have a PM^3 but whether it is large or small varies. Most have a metaconule present on M^1 and all have the premetacrista on M^3, but both teeth vary in their development (table 11). The large African *Tadarida africana*, *T. fulminans*, and *T. lobata* join together at 0.500, after *fulminans* and *lobata* form a pair first at 0.430. The close similarity of these three bats has been noted by several authors. Peterson & Harrison (1970) and Peterson (1974) compared and contrasted *lobata* with the other two, and Harrison (1971) compared *africana* with *lobata* and *fulminans*. These three may be slightly more derived than the other three because of their narrower wing tips, more finely wrinkled lips, and less development of the metaconule on M^1 and premetacrista on M^3.

At 0.520, *T. teniotis* and *T. australis* join together. Hill (1961) thought *T. australis* was more similar to *T. aegyptiaca* in spite of its greater size, but he also mentioned that it should be thought of as "an isolated and outlying member of that subgenus [*Tadarida*]." McKean & Calaby (1968) concluded that *australis* is closely related to *T. kuboriensis*, another Australasian molossid, but that its skull is longer than that of *kuboriensis*. Both shape-clustering analyses place *australis* closest to *teniotis*. Because of this and because *teniotis* is a widespread species, I think *australis* and possibly *kuboriensis* are Australasian relatives of *teniotis*. *Tadarida teniotis* is found between latitudes 20° and 40° N in the Palearctic region and is the only molossid to live this far north all year.

The three large African *Tadarida* join the *teniotis-australis* pair at 0.670. Koopman (1975) placed the large *africana*, *fulminans*, *lobata*, and *teniotis* in his *T. teniotis* group of large forms. Thomas (1891) mentioned that some relationship with the large African forms and *teniotis* exists, particularly with respect to *lobata*. This last affinity was reviewed by Peterson & Harrison (1970) and Peterson (1974). The three seem equally derived over *teniotis* because they retain only four lower incisors and a less than completely shaped N on the M^3. The PM^3 is well developed in all three, though possibly less so in *africana*, the largest species of *Tadarida*. These six molossids are nearest neighbors of one another

and are most highly correlated with one another, but two other bats are phenetically related to them, namely *Tadarida brasiliensis* and *Tadarida aegyptiaca*. Aellen (1970) noted that the shape of the baculum in *T. teniotis* resembles that in *T. brasiliensis*.

Koopman (1975, p. 424), after clearly demarcating species in the subgenus *Chaerephon*, restricted "typical *Tadarida* to the *teniotis* group, *aegyptiaca* and *brasiliensis*." These last two bats have a definite similarity with *Tadarida*: *T. aegyptiaca* is most highly correlated with *teniotis*, and *brasiliensis* is highly correlated with *aegyptiaca*. The two are also each other's nearest neighbor, size-out, but their next nearest neighbors are species of *Mormopterus*; hence, their placement on the phenogram. I discuss these two bats later, but phenetically they are similar to both *Tadarida* and *Mormopterus*.

Tadarida kuboriensis joins the five *Tadarida* at 0.690. This bat is nearest *brasiliensis* (0.578) size-out, but most highly correlated with *australis*. *Tadarida kuboriensis* averages nearer *Tadarida* than to any other genus on the phenogram. Actually *australis* and *kuboriensis* are similar, and in an analysis where only raw data are used (no codes or ratios) *kuboriensis* is closest to *australis* in all three clustering methods. McKean & Calaby (1968) have also pointed out the similarity between these two species, and Koopman (1975) included *kuboriensis* in *australis*. Why a rather great size-out distance exists between the two Australasian *Tadarida* (0.602) is difficult to explain.

New World *Tadarida* (without *T. brasiliensis*) form a distinct cluster of four species: *aurispinosa*, *femorosacca*, *laticaudata*, and *macrotis*. The first juncture occurs at 0.420, connecting *aurispinosa* and *femorosacca*, a pair which had a history of taxonomic confusion, until Carter & Davis (1961) resolved the situation. *Tadarida laticaudata* joins the two at 0.480, and *T. macrotis* joins the three at 0.570. The four form what Miller (1902) called the genus *Nyctinomops* (*Tadarida* at the time was called *Nyctinomus*) and what Shamel (1931) named the *T. macrotis* group of New World *Tadarida*. Because these four species form a distinct group in this analysis, I recommend that Miller's name, *Nyctinomops*, be resurrected. This group is distinct from the *T. brasiliensis* group of Shamel because of its short second phalanx of digit IV and its narrower rostrum, characters also included in this analysis. The derived traits of the *macrotis* group over *brasiliensis* are the loss of I_3, the shortening of the second phalanx of digit IV, the well-joined ears, and the slightly narrower palatal emargination (table 11). Exactly how these four species I now call *Nyctinomops* are phylogenetically related with the remaining species of *Tadarida* is unclear. Although a phenetic connection with them via *T. brasiliensis* is logical because of the latter's close geographic occurrence with the *macrotis* group, there is only slight support from the size-out analysis and little more from correlation. The *macrotis* group (*Nyctinomops*), however, averages closer to the Old World *Tadarida* than to any other genus (table 8). Specific neighbors which are almost as close are members of *Chaerephon* (including *ansorgei*) and *T. teniotis*. Because of the similarity of the anterior palatal emargination with certain species here included in *Chaerephon*, Koopman (1975) did not include these *Tadarida* from the New World (or *T. australis* and *T. kuboriensis*) with his "typical *Tadarida*." The difference in the configuration of the wing tips of the *macrotis* group (*Nyctinomops*) and that of *Chaerephon* is considerable, even greater than the difference between that of the former and of *T. brasiliensis* (table 6).

The largest species of *Nyctinomops* is *macrotis* (GSL = 23.3 mm), and it ap-

pears to be the largest in a graduated size series starting with *laticaudata* (GSL = 18.0 mm) shown in Figure 15. Because of this graduated series, I think a close phylogenetic relationship of *macrotis* with a molossid of another group is unlikely. The fact that *macrotis* is most highly correlated with *Otomops martiensseni* is, I believe, due to convergence. *Otomops martiensseni* is also the largest member of a graduated series of species of *Otomops* (the smaller specimens were not available for drawing; fig. 13). There are also several differences between the two genera in the primitive-derived traits. Species of *Otomops* have extremely deep basisphenoid pits, finely wrinkled lips, no metaconule on M^1, and broad wing tips (table 11).

Otomops here consists of four species of medium to large size (GSL = 19.5 to 27.0 mm). *Otomops secundus* from New Guinea joins *O. wroughtoni* from India at 0.330. The large African *O. martiensseni* joins the *secundus-wroughtoni* pair at 0.480, and the small Papuan *O. papuensis* joins the other three at 0.580. Closest neighbors of each species both in size-out and correlation are congeners. Simpson (1945) placed *Otomops* in the genus *Tadarida* (*sensu lato*). When codes and ratios are omitted from the analysis, some of the species of *Otomops* do have nearest neighbors among species of *Tadarida* and *Nyctinomops*, especially *T. teniotis*. Whether the similarity with *teniotis* is one of close phylogenetic affinity or convergence, as with *N. macrotis*, is unknown. Because *teniotis* is a large species of *Tadarida*, I suspect that the phylogenetic relationship is more likely to be with a smaller ancestor of *teniotis*. The phenetic relationship with *teniotis* is not a strong one.

Last is the juncture of *Eumops perotis* with *Tadarida* and *Tadarida*-like bats at 0.920. Though the nearest or most highly correlated neighbors of *E. perotis* are congeners, species of *Tadarida*, *Nyctinomops*, and *Otomops* average closer. Distance from nearest neighbor, *E. bonariensis*, is 0.702, the greatest distance from any nearest neighbor, but the neighbor most highly correlated is *E. underwoodi* at 0.795, a substantially high correlation. *Eumops perotis* is probably ecologically convergent with the *Tadarida-Nyctinomops-Otomops* group to which it is attached. *Eumops perotis*, like *N. macrotis* and *O. martiensseni*, is the largest in a graduated series of congeneric species that look very much alike (fig. 20). All three of these large bats have long, thin jaws, and large, slouched ears joined by a band over the nose and wrinkled, expandable lips. *Eumops perotis* and *N. macrotis* both have narrow wing tips, whereas *O. martiensseni* has broad ones. All three tend to live in arid regions and may migrate to or inhabit more temperate regions (*E. p. trumbulli* is more mesic), and I suspect all three eat soft-bodied creatures like moths. *Eumops perotis*, *N. macrotis*, and *O. martiensseni* seem to have converged toward a mutual and successful skull and body design which meets the needs of their similar life styles and feeding habits. *Eumops perotis* does have the additional derived characters of lacking the palatal emargination and having less-developed PM^3 and M^3 (table 11).

In the next assemblage, all of the species of *Chaerephon* are joined together at 0.540 (fig. 22). This low numerical juncture means that the bats of this group are less dispersed morphologically than typical *Tadarida*, that is, they look more like one another. Species of *Chaerephon* are medium in size and have thin jaws like those of *Tadarida* but are different from *Tadarida* in other jaw characteristics. All have four lower incisors, but the posterior commissures on M^3 and PM^3 in most species of *Chaerephon* are slightly less developed than those teeth in *Tadarida*, and the metaconule on M^1 is less distinct. *Chaerephon* is a slightly more derived

genus of molossids than *Tadarida*, not only because of dental traits but also because the palatal emargination is only a small notch in most of the species, and most have well-joined ears (table 11).

Features in addition to palatal emargination, and M^3 and PM^3 development which are classical characters used to distinguish *Chaerephon*, were used to determine the species positions on the phenogram (fig. 22). The majority of bats in this cluster group in much the same fashion even when the classical characters, described by codes, are removed from the analysis. Nearest neighbors both in size-out and correlation analyses are species of *Chaerephon*.

At the top of the cluster (fig. 22) *ansorgei* and *bivittata* join at 0.260. Recently, both Randolph Peterson and Judy Eger (personal communication) mentioned that they think these two are synonymous, and the low distance at which the two bats join in my study supports their idea. The two are each other's closest neighbor in both size-out correlation analyses. Koopman (1975) mentioned that *ansorgei* and *bivittata*, along with *bemmelini*, are similar, but he placed them in *Tadarida* where they must go if *Chaerephon* is conventionally defined by the shape of the palatal emargination. Differences among these three bats are discussed in the first section, but they may be slightly more primitive species of *Chaerephon* (table 11). Hayman & Hill (1971) placed *ansorgei* in *Tadarida* and *bivittata* and *bemmelini* in *Chaerephon*. I recommend that all three are species of *Chaerephon*.

Chaerephon aloysiisabaudiae joins the *ansorgei-bivittata* pair at 0.350, followed by *russata* at 0.360. Peterson (1969) thought *aloysiisabaudiae* to be the closest relative of *russata*. Additional comparisons and similarities between these two and with *bivittata* were pointed out by Peterson (1967, 1971b) and by Fenton & Peterson (1972). Both *aloysiisabaudiae* and *russata* are nearest *ansorgei* in size-out distance, but although *russata* is most highly correlated with *ansorgei*, *aloysiisabaudiae* is most highly correlated with *russata*.

Chaerephon major and *C. nigeriae* form a pair at 0.370 before joining the cluster containing *ansorgei, bivitatta, aloysiisabaudiae*, and *russata* at 0.390. As for opinions concerning relationships of these two bats by previous authors, Rosevear (1965) noted that the skull of *major* is the same general form as that of *pumila* but is larger, whereas that of *nigeriae* is broader and flatter than that of *major*. Both *major* and *nigeriae* are nearest *bivittata* in size-out distance. In correlation, *major* is most highly correlated with *chapini* and *nigeriae*, with *russata*.

Chaerephon pumila joins the cluster at 0.400, followed by *chapini* at 0.430. Kock (1969) thought *chapini* and *pumila* should be regarded as conspecific, and although Koopman (1975) disagreed with that conclusion, he thought that the two are closely related. This analysis places both as nearest neighbors (size-out) of *bivittata*. *Chapini* is most highly correlated with *major* and *pumilia* is most highly correlated with *chapini*.

Chaerephon bemmelini joins the cluster of species of *Chaerephon* at 0.480. Peterson (1971b) believed that the closest relative of *bemmelini* is *bivittata*. This study agrees with that conclusion in both shape analyses. This bat, like *bivittata*, has been frequently allied with species of *Tadarida* (Thomas, 1903; Koopman, 1975).

The last two forms to join bats in this cluster are two Indo-Australian species, *plicata* and *johorensis*, at 0.490 and 0.540, respectively. Hill (1961) reported *johorensis* to be externally much like *plicata* (except for a complex ear juncture); its skull differs from that of *plicata* by having a more flattened rostrum. He

compared only Indo-Australian members of *Chaerephon*. *Chaerephon johorensis* is nearest in distance to *chapini* and most highly correlated with *bemmelini*, whereas *plicata* is nearest *bivittata* and most highly correlated with *pumila*.

Miller (1907) claimed that *Chaerephon* closely resembles *Tadarida* (including *Nyctinomops*) except in the shape of the palatal emargination (the first are shallow, the second deep). Species of *Chaerephon* and *Tadarida* have had a long history of being included in or excluded from a single taxon. In my study each is a distinct cluster, but the two do have many characteristics in common. The fact that *ansorgei*, *bivittata*, and *bemmelini* have been difficult to place indicates to me that they are probably phylogenetically related to both *Tadarida* and *Chaerephon*. The last bat, *bemmelini*, along with the Indo-Australian species, has a slightly more primitive dental pattern than do most of the species of *Chaerephon* (table 11).

One of the largest species of *Chaerephon*, *aloysiisabaudiae*, has an elongate, narrow rostrum and a distinct metaconule on M^1, features more typical of *Tadarida*. If large size does mark the end of a shape line, then *aloysiisabaudiae* may be paralleling the *Tadarida*-like shape. It could be that *Chaerephon* is the small-sized counterpart of *Tadarida* and that to become a larger *Chaerephon* is really to become *Tadarida*-like.

The other large bat classically placed in *Chaerephon* is *jobensis*. This bat, although its tooth configuration is characteristic of species of *Chaerephon*, has features of the jaw and skull which are similar to those of *Mops*. I think *jobensis* has taken advantage of a way of life different from that of typical species of *Chaerephon* because it is located in a geographical area where there are no species of *Mops*.

Species of *Mops* form an assemblage about as dispersed as species of *Chaerephon* and consist of bats which have medium to thick jaws, robust skulls, and body sizes that vary from small to large (fig. 22). These bats are positive on axis II and axis IV but negative on axis III (fig. 4). Because of their jaw structure, I suspect that species of *Mops* eat hard-bodied insects, like beetles, but actual data are scanty. Primitive and derived configurations of the teeth are not clear. Most species have four lower incisors (one has only two), but variation in PM^3 ranges from well developed to vestigial and even absent in two species. Diminution of PM^3 does not always occur with the diminution of the posterior commissure on M^3. All species have at least a small notch which is a remnant of the palatal emargination, shallow to deep basisphenoid pits, and wrinkles on the lips. All but one (*niangarae*) have joined ears (table 11).

At 0.520, two bats, *C. jobensis* and *M. condylura*, join the main cluster of species of *Mops*. *Chaerephon jobensis*, as one might expect, has the more primitive tooth configuration: PM^3 is moderately developed and M^3 is well developed as in *C. johorensis*. Although *jobensis* is a large species of *Chaerephon*, it is like *Mops* because of its well-developed sagittal and lambdoidal crests and thick jaws (fig. 12). The bat with which *jobensis* joins, *M. condylura*, has been suggested by Rosevear (1965) to be intermediate between *Chaerephon* and *Mops* because *condylura* has a smaller anterior emargination and slightly better developed M^3 than most species of *Mops*. There are species of both *Mops* and *Chaerephon* that have only a notch remaining of the palatal emargination, so that this character is not a good one to use in determining which is more primitive or derived. *Mops condylura* has distinctly thick jaws and a well-

developed sagittal crest, characters shared with other species of *Mops*. The last upper molar retains a slight posterior commissure (less than half the length of the second ridge), and PM³ is vestigial. Both are traits more derived than those of species of *Chaerephon*, but may be less derived than those of other species of *Mops*.

If *jobensis* and *condylura* are intermediate between *Chaerephon* and *Mops*, what is the nature of their relationship with the two groups? *Chaerephon jobensis* is considered by Hill (1961) to be a closely related but distinct Australasian representative of *C. plicata*. He wrote (p. 54), "The skull differs little from that of *T. plicata* in structural details but is rather more heavily built. The anterior upper premolar is sandwiched tightly between the canine and PM⁴; the anterior lower premolar is only slightly reduced." *Chaerephon jobensis* is closest to species of *Mops* both in size-out and correlation, but because of its large size and *Chaerephon*-like teeth, I suspect it is derived from earlier, smaller bats of the genus *Chaerephon* and has more recently taken to eating harder-shelled prey.

Mops condylura, on the other hand, is closest to *M. demonstrator* in size-out and correlation analyses but also is of medium size and has *Mops*-like teeth. Koopman (1975), also noticed the similarity between *condylura* and *demonstrator* and thought the two are closely related. *Mops condylura* appears to be a widespread and adaptable bat with several related forms. It may well have a close relationship with *Chaerephon* as Rosevear (1965) suggested, but here *condylura* is assigned to *Mops*. Koopman (1975) and Hayman & Hill (1971) concurred with this assignment.

The main cluster of species of *Mops*, like those of *Chaerephon*, are bats connected by small distances. These thick-jawed bats have no nearest neighbors, by any of the three clustering methods, outside their group and maintain a distinct, compact cluster. Like the case with the cluster of species of *Chaerephon*, even when raw data alone are used, a similar compact cluster of species of *Mops* results.

Recently, Koopman (1975) placed five molossids in the *Tadarida* subgenus, *Xiphonycteris*, because they share the reduced M³ and well-developed anterior emargination. My analysis does not separate these molossids from other species of *Mops* which have a reduced M³ but small palatal emargination. Two of these five, *brachyptera* and *thersites*, pair at 0.330. Each is the other's nearest or most highly correlated neighbor. The pair is joined by *trevori* at 0.390 and by *niangarae* at 0.470, two included in the *midas* group of large forms of *Tadarida* (*Mops*) of Koopman (1975). These four bats have all been coded for having moderately developed PM³ and M³ with less than one-half development of the posterior ridge present. Although *trevori* is nearest *thersites*, size-out, and most highly correlated with *niangarae*, *niangarae* is both nearest to and most highly correlated with *trevori*. Whether *niangarae* is a distinct species or synonymous with *trevori* has been a matter of conflict among previous authors (Koopman, 1965; Hayman & Hill, 1971; Peterson, 1972; Koopman, 1975). Peterson discussed fully the relationship between *trevori* and *niangarae*, synonymized the latter with the first, and subsequently compared *trevori* with *congica*, another similar large bat. Koopman (1975) agreed "reluctantly" to this arrangement, but until more specimens can be collected, I am inclined to keep *niangarae* as a distinct taxon because of its more robust jaw, separated ears, and only average distance to nearest neighbor *trevori* (0.417). Peterson (1972) thinks the condition of the ears

in the type and only known specimen was distorted in preparation and that the difference in robustness is due to sexual dimorphism, both of which are quite possible.

In the next subgrouping of species of *Mops*, *demonstrator* and *niveiventer* pair at 0.350, joined by *midas* at 0.420 and *congica* at 0.460. The first two are each other's closest neighbor in both shape analyses. *Mops midas* and *congica* are both nearest *demonstrator* in distance, but are each other's most highly correlated neighbors in correlation. All four of these bats have been coded for having a small PM³ (vestigial in *demonstrator* and *niveiventer*) and for the complete lack of a posterior ridge on M³. This dental configuration could be construed as being slightly more derived than that of the *brachyptera-niangarae* subgroup. Also, *midas* and *congica* are the largest species of *Mops*. Koopman (1975) put *demonstrator* and *niveiventer* into his *T. (M.) mops* group of small forms, and *congica* and *midas* into his *T. (M.) midas* group of large forms. Koopman thought that *demonstrator* is most closely related to *niveiventer*, but emphasized that the latter has often been confused with *condylura*. He suggested the probability of intergradation between *niveiventer* and *demonstrator*. Hayman & Hill (1971) mentioned that *congica* looks like a large specimen of *condylura*, a resemblance which only remotely unites the large and small species in this subgroup. Although at one time *trevori* was included as a subspecies of *congica* by Koopman (1965; the first being a savannah species and the second a forest-living one), Peterson (1972) separated the two as distinct species. The connection of the first subgroup containing *trevori* and *niangarae* and the second containing *congica* and *midas* occurs at 0.520.

Three small species make the next subgroup: *Mops leonis* pairs with *M. nanula* at 0.390, followed by *Xiphonycteris spurrelli* at 0.450. These three have shallow basisphenoid pits and retain PM³ but have lost the posterior commissure on M³. *Xiphonycteris spurrelli* is distinctive because it has a large PM³ and only two lower incisors. (Randolph Peterson told me that he has recently seen specimens of *spurrelli* with two, four, and six lower incisors.) In distance, *nanula* and *spurrelli* are nearest *leonis*, and *leonis* is nearest *nanula*. In correlation, *nanula* and *spurrelli* are most highly correlated with *leonis*, but *leonis* is most highly correlated with *spurrelli*. Koopman (1975) noted the similarity between *spurrelli* and *nanula* and placed *nanula*, *leonis*, *brachyptera*, *thersites*, and *spurrelli* into *Tadarida (Xiphonycteris)*. Others have noticed the resemblance among these bats. Rosevear (1965) mentioned the similarity between *leonis* and *thersites*, the skull of the former being "slighter in general appearance" than that of the latter. Hayman & Hill (1971) stated that the helmet-like appearance of the skull of *Xiphonycteris spurrelli* occurs in several species of *Mops*, and the authors intimate a resemblance between *spurrelli* and *nanula*, a small species of *Mops*. Koopman thinks these two small bats may be conspecific. I see no reason to keep *Xiphonycteris* as a valid name, even as a subgenus; the name *Mops spurrelli* is sufficient. This subgroup of three joins the first two subgroups at 0.520.

The final two species of *Mops* are Indo-Australian. *Mops mops* and *M. sarasinorum* pair at 0.400 and join the main body of the species of *Mops* at 0.550, a juncture slightly less than that of *C. jobensis* and *M. condylura*. *Mops mops* and *M. sarasinorum* are not only each other's nearest and most highly correlated neighbors, but both have a slightly more derived toothrow than that in the African species: neither has a PM³ and their M³ is highly reduced (table 11).

Their next nearest neighbors are species of African *Mops* rather than species of Indo-Australian *Chaerephon*, including *C. jobensis* (table 7).

Chaerephon and *Mops* join at 0.630 units, a distance less than that joining the Old and New World *Tadarida* (0.750). Originally designated as independent genera, *Chaerephon* and *Mops* have more recently been thought of as subgenera of *Tadarida* (Simpson, 1945; Ellerman & Morrison-Scott, 1951), but these two do form distinctive clusters in my multivariate study. The trend in diminution of PM^3 and the posterior ridge on M^3 are losses in the toothrow which occur in the New World genera as well.

Mormopterus and *Mormopterus*-like bats follow the cluster of species of *Mops* in the phenogram (fig. 22). In general, *Mormopterus* is a genus in which bats are small, have a well-developed M^3, tall posteriorly curving coronoid process, medium-thick jaws, separated ears, shallow basisphenoid pits, and unwrinkled lips. These bats may take soft and hard prey of small size, though few data are available. On the three axes of the PCA, they are located in the center of axis II, toward the positive end of axis III, and are slightly positive on axis IV (fig. 4).

Species of *Mormopterus* are distinct from other molossids because of the maintenance of the large, invariable, N-shaped M^3; while both PM^3 and I$_3$ are variable in their presence in the toothrow. Often in other molossids, PM^3 and posterior cusp of M^3 co-vary in absence or presence. I consider all species of *Mormopterus* to be primitive molossids, but no living species have all the primitive dental characteristics. The two African-Malagasy *Mormopterus* have six lower incisors but no PM^3, whereas the three small Australasian species have only four lower incisors but maintain a small PM^3. *Mormopterus doriae*, from Sumatra and not available for my study, is said to bear six incisors but no PM^3 as in the African forms (Hill, 1961). *Sauromys* from Africa has four lower incisors and a small PM^3 like the three small Australasian *Mormopterus* and *Mormopterus beccarii*, the largest species of *Mormopterus* (Australasian). I consider the New World forms of *Mormopterus* (*kalinowskii, phrudus,* and *minutus*) to have the most derived tooth formula because they have lost both I$_3$ and PM^3. *Platymops* from Africa, another bat more distantly related to this cluster, has also lost I$_3$ and PM^3 (although the latter is sometimes present as a spicule which Peterson [1965] thinks is a milktooth). If *Platymops* is considered a species of *Mormopterus*, it would be the most derived Old World member.

Because of the variation in tooth configuration in species of *Mormopterus*, one might wonder about which teeth are lost through time for members of this genus. Often, teeth are eliminated by a shortening of the jaw or an enlargement of other teeth or both at once. The last upper molar is not diminished in this particular genus of small bats; only teeth in the anterior part of the jaw are the ones lost. Apparently the posterior cusp on M^3 at the posterior part of the jaw, a part where much force occurs during chewing, is more useful than those anteriorly. The complete M^3, combined with the unusually elevated condyle above the toothrow, may give a great advantage to these small bats in cutting up their prey.

Prior to the 0.420 line, the three New World species (*kalinowskii, minutus,* and *phrudus*) join together, and just past this line, the three Australasian species (*loriae, norfolkensis,* and *planiceps*) form a cluster (fig. 22). These last three may be confused taxonomically (Johnson, 1959; McKean & Price, 1967). At 0.480, these six small-sized bats (GSL = 13.0–15.5 mm) join together to form the core of

the *Mormopterus* cluster. The relationship between these two similarly shaped but geographically distant subgroups of *Mormopterus* is, I suspect, one of recent common ancestry rather than an overall convergence of 76 characters toward a small-sized similarly shaped molossid.

Sauromys joins these six species of *Mormopterus* at 0.520 and appears more similar in shape to these bats than to any other flat-headed bat such as *Platymops*, with which *Sauromys* was considered to be congeneric at one time (Harrison, 1962). *Sauromys* is closest to *Mormopterus norfolkensis* in all three clustering analyses and shares several of the traits listed in Table 11 with Australasian *Mormopterus*. The condition of the ears of *Sauromys* is more derived than that in *Mormopterus* because they are not widely separated; the ears only just join at the bases to form a V-shaped valley. I consider *Sauromys* a subgenus of *Mormopterus* that has adapted to living under desert conditions and in narrow roosts. Peterson (1965) suggested that *Sauromys* is closest to *Tadarida* (including *Nyctinomops*) and *Mormopterus* than to any other molossid genus and is quite distinct from *Platymops*. Prior to Peterson's report, Harrison (1962, p. 763) had written that *Sauromys* was "an evolutionary connecting form" between *Tadarida aegyptiaca bocagei* (which he called primitive) and *Platymops* (which he called specialized for narrow crevices). Although my analysis cannot support or refute this idea, it does cluster *Sauromys*, *Platymops*, and *T. aegyptiaca* in the same general area of the phenogram; hence, the bats have some phenetic similarity.

At 0.530 *M. acetabulosus* from Madagascar and eastern Africa joins the main cluster of species of *Mormopterus*, bats to which it is more similar in shape than to the other species of *Mormopterus* from Madagascar, *M. jugularis*. Nearest neighbors of *acetabulosus* are New World *Mormopterus*.

Two species of *Tadarida* join the cluster of species of *Mormopterus* at 0.560. These two bats, *T. aegyptiaca* from the Old World and *T. brasiliensis* from the New World, form a pair before the 0.420 line. This low phenetic juncture between these two bats provides an interesting, unexpected similarity between molossids of the Old and New Worlds. Presently, both bats are widespread in their respective hemispheres: *T. aegyptiaca* inhabits most of Africa and southwestern Asia, while *T. brasiliensis* is found from about 40° N latitude in North America through Central America to about 40° S in South America. Similarity in shape could be due to convergence because of similar life styles; both are able to tolerate arid conditions (Harrison, 1962; Krutzsch, 1955; Hayward, personal communication) and are able to seek shelter under flakes of rocks and in narrow crevices. Their jaw proportions are similar and neither has a very narrow or very broad wing tip. *Tadarida brasiliensis* may be the more primitive molossid because it maintains six lower incisors (Slaughter, 1970), although the third lower incisor is small and often variable in its appearance (Glass, 1953), and it has only shallow basisphenoid pits. Both maintain PM^3 and N-shaped M^3 and both have separated ears and wrinkled lips (table 11). Although the separated ears is the only really different trait from the other species of *Tadarida*, the ears are not widely separated or short and erect as in species of *Mormopterus*, but larger and more forward-facing as in other *Tadarida*.

It is an intriguing occurrence that *T. brasiliensis* is represented by my analysis as being more similar to an African bat rather than to other New World species (*Nyctinomops* or *Mormopterus*). A close phylogenetic relationship between the two, *brasiliensis* and *aegyptiaca*, cannot be ruled out. A recent Old World-New

World exchange in the genus *Tadarida* (*sensu lato*) has heretofore been considered improbable relative to some vespertilionid Old-New World relationships (Koopman, 1970). However, my analysis, where I have tried to remove size differences among the bats, would support a more recent phylogenetic relationship between species of *Tadarida* in the Old and New World. Indeed, the resemblance between a small subspecies of *T. aegyptiaca*, *T. a. bocagei*, and *T. brasiliensis* is strong and supports the suspicion of a close phylogenetic relationship (fig. 23).
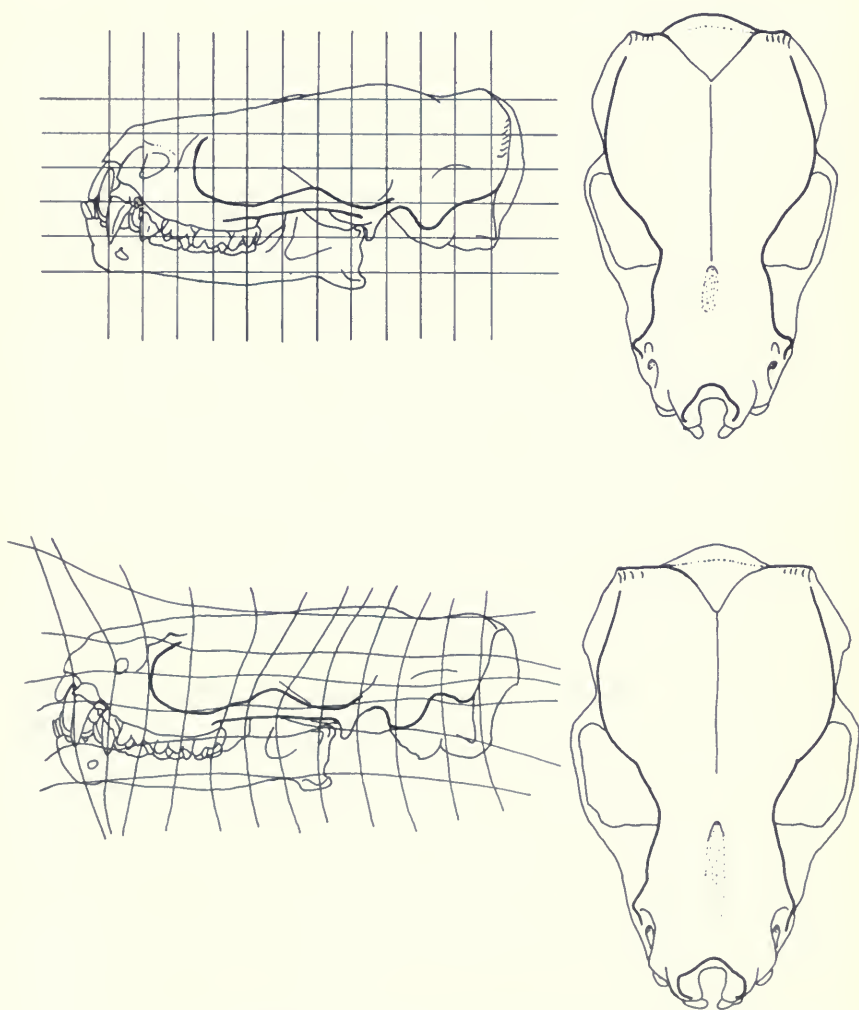
FIG. 23. Pictorial comparison of proportions by regular and deformed coordinates of *Tadarida brasiliensis* (top) from the New World and *Tadarida aegyptiaca bocagei* (bottom) from the Old World. The coordinates are regular for the lateral view of *brasiliensis* and deformed for *aegyptiaca* (for method, see Thompson, 1971; Simpson et al., 1960). The two bats are especially similar from the dorsal view, and coordinates are not drawn.

As to the relationship of the *aegyptiaca-brasiliensis* pair with species of *Mormopterus* and species of *Tadarida*, good evidence exists that they are phenetically similar to each. Indeed, the pair share the same condition of the ears with *Mormopterus*. Next nearest neighbors (size-out distance) of *aegyptiaca* and *brasiliensis* is a New World species of *Mormopterus* and next nearest are species of *Tadarida*. Although a relationship between *brasiliensis* and New World *Mormopterus* has been mentioned by de la Torre (1956) and Handley (1956), *Tadarida brasiliensis* differs by having more wrinkling on the lips and the presence of PM^3 and I_3 (table 11). I suspect the similarity between the *aegyptiaca-brasiliensis* pair and species of *Mormopterus* and *Sauromys* in the flattening of the cranium affects the placement of the pair on the phenogram.

Though in the size-out analysis the *aegyptiaca-brasiliensis* pair averages closer to *Mormopterus* (0.562), it is almost as close to *Tadarida* (0.570). I think the relationship with the latter is substantial. In size-out distance, *brasiliensis* is the nearest neighbor of both *aegyptiaca* and *kuboriensis* and second nearest of *australis*. In correlation, *aegyptiaca* is most highly correlated with *teniotis*, then *brasiliensis*, *fulminans*, and *australis*; and *brasiliensis* is second most highly correlated, after *aegyptiaca*, with *Mormopterus kalinowskii* (table 7). Also, in several of the major morphological characters (table 6), *aegyptiaca* and *brasiliensis* are more in line with the variation in *Tadarida* than in *Mormopterus*.

The largest species of *Mormopterus* joins the cluster at 0.700. *Mormopterus beccarii* (GSL = 18.0 mm) from Australasia is nearest the Malagasy *M. jugularis* (GSL = 16.5 mm) at 0.595, but the nearest neighbor of *jugularis* is actually *norfolkensis* (0.483). The phenetics are slightly distorted here by the phenogram, but the larger or Malagasy forms are more distant from or less similar to the smaller species of *Mormopterus* (table 7). Although Hill (1961) mentioned that *beccarii* is closely related to *planiceps* because of a similar cranial profile and similar development of PM^3 and PM_3, my analysis does not support that relationship. *Mormopterus beccarii* is one of the most distant species of *Mormopterus*. It is likely that because of its large size, *beccarii* is allometrically out of proportion with other *Mormopterus* for structural reasons intrinsic with its large size. *Mormopterus beccarii* could also be, according to Cope's Rule (see Stanley, 1973), the end of a line of related shapes and not one closely related phylogenetically with the ancestor of the *Mormopterus* line.

Platymops is related phenetically to the *Mormopterus* cluster and joins it at about 0.780 (see also placement in table 6). Nearest neighbors of this flat-headed African bat are *acetabulosus* at 0.673, an African-Malagasy *Mormopterus*; *minutus* at 0.682, a New World form; and *Sauromys* at 0.771, another African flat-headed bat. Peters (1878), who first named the species now called *Platymops setiger*, originally described it as *Mormopterus setiger*. It is the more derived of the two Old World flat-headed bats and other species of *Mormopterus* because PM^3 is lost and the lips appear to be wrinkled and covered with unusually thick hairs (wrinkling was hard to code because of the hairs). A close phylogenetic lineage from a primitive *Mormopterus* via *Sauromys* to *Platymops* is not supported by phenetics. It is more likely that the two flat-headed molossids diverged separately from a primitive *Mormopterus*-like bat. *Platymops* and *Sauromys* are not each other's closest neighbors in the shape analyses, and both are large compared with most species of *Mormopterus*. (*Sauromys* is the nearest size-in neighbor of *Platymops* but at a distance of 0.724; table 7.) I suggest that *Sauromys* and

Platymops be considered subgenera of *Mormopterus*, but they would be the most derived species of the genus.

With the exception of the two species of *Tadarida* attached to this group, all the species of *Mormopterus*, *Sauromys*, and *Platymops* have closest neighbors within the group. Nearest neighboring genera of *Mormopterus* (including *Sauromys* and *Platymops*) are given in Table 8.

Seven bats representing four classical genera (*Molossops*, *Neoplatymops*, *Cynomops*, and *Myopterus*) are assembled in the next cluster (fig. 22). They have been called the conglomerate group in a previous section. On the whole, the cluster is not as dispersed as one might think if, indeed, four genera are involved. These bats tend to have thick dentaries, broad faces, widely separated short, erect and laterally facing ears, no anterior emargination of the palate, and little or no development of wrinkles or basisphenoid pits (table 11; *Myopterus* is an exception in this last trait as it has very deep pits). *Myopterus* and *Neoplatymops* have only medium-narrow wing tips, whereas *Cynomops* has narrow ones and *Molossops* has very broad ones. All are positive on axis II and III and slightly positive on axis IV (fig. 4). I suspect that the larger species of *Myopterus* and *Cynomops* are eating hard items, but less certainty exists for the smaller species, although all have rather thick dentaries.

Based on tooth characteristics, the small *Neoplatymops* has the most primitive condition with four lower incisors, presence of small PM^3, and presence of a completely developed posterior commissure on M^3. Most derived of the cluster is the African *Myopterus* with only two lower incisors, no PM^3, and no posterior ridge on the M^3. The two remaining genera, *Molossops* and *Cynomops*, have tooth traits which are between the primitive and advanced states and can to some extent be graded. Although *Molossops* has only two lower incisors and no PM^3, it maintains a slight posterior ridge on M^3 (of less than one-half length). *Cynomops*, on the other hand, though it has four lower incisors and no PM^3, has completely lost the ridge on M^3. Goodwin (1958) noted that the incisor number in *Cynomops greenhalli* is variable (two in the male type and four in the female topotype). Warner et al. (1974) presented chromosome data in which *greenhalli* and *abrasus* (*C. brachymeles?*) have 34 chromosomes instead of the primitive number of 48. Also, *Cynomops* contains the largest of the species of *Molossops* and *Cynomops*.

Neoplatymops joins *Molossops* at 0.490. Small and primitive, *Neoplatymops* is distinguished by Peterson (1965) as one of the flat-headed molossids and worthy of generic status. Historically, this bat has been called *Molossops* and *Cynomops*. *Neoplatymops* and *Molossops* are closest neighbors in both shape analyses. The two, relative to all other molossid genera, do not require separate generic status in my study. There are several differences in the teeth and external appearance of these two bats (see Peterson, 1965), but their shape and, I think, habits are basically similar. Not only have the two been thought similar in the past, but 0.490, a relatively low distance, indicates substantial similarity among two bats in my analysis. *Neoplatymops* here is probably more logically classified as a subgenus of *Molossops*.

The three species of *Cynomops* cluster at 0.340, forming a distinct entity. The three join *Neoplatymops-Molossops* at 0.610. Species of *Cynomops* are each other's nearest neighbor in both size-out and correlation, but as an entity of three they are nearest (size-out) *Molossops* and *Neoplatymops* (table 8). In the

past, species of *Cynomops* have been called *Molossops*, *Molossus*, *Promops*, and *Myopterus*. *Cynomops* joins *Molossops* at 0.610, and although this number is not a small distance, is about the same as the distance at which other molossid genera form (for example, *Tadarida* and *Otomops*). Peterson (1965) described the differences between *Cynomops* and *Molossops* and considered them to be separate genera, but I think their shapes are similar enough to be included within one genus. Gardner (1977) reported that *Molossops* has 42 chromosomes and differs from the chromosome number of 34 in *Cynomops*. He noted, however, that variation in chromosome number among members of the same molossid genus does occur, for example in *Eumops*. He asked the following question (p. 548): "Does recognition of *Molossops* and *Cynomops* at the generic level better reflect the true relationship between these taxa, or does it obscure their close phylogenetic affinity?" My study does little more to clarify the situation, but relative to other molossid genera already described here, *Molossops* including *Neoplatymops* and *Cynomops*, is about as phenetically dispersed. Subsequently, I list *Cynomops* as a subgenus of *Molossops*.

Neoplatymops, relative to *Molossops* and *Cynomops*, has been described by Peterson (1965, p. 21) as representing an "intermediate condition between *Tadarida* [excluding *Mormopterus*] on the one hand and the *Molossops-Cynomops* complex on the other" (based on palate configuration). He suspected that both *Molossops* and *Cynomops* could be derived from *Neoplatymops* because of dental characteristics. Possibly, species of *Cynomops* are the most derived bats of this complex, not so much by tooth criteria but by their narrower wing tips, lower chromosome number, and large-sized species. The largest bat here is *Cynomops brachymeles* which is definitely in a graduated series of similar bats (fig. 17). This large bat could mark the end of this particular *Molossops*-shape line in the New World. The most closely related bats to *Molossops* (*sensu lato*), other than *Myopterus*, in both shape analyses are species of *Mormopterus*, bats with which *Molossops*-like bats share several external morphological features (table 7). Nearest neighboring genera of *Molossops* (plus *Cynomops* and *Neoplatymops*) are listed in Table 8.

The two species of *Myopterus* found only in the Old World, *M. albatus* (GSL = 23.5 mm) and *M. whitleyi* (GSL = 17.0 mm), join together at a distance of 0.540 units. In the size-out shape analysis the two are more similar to each other than to any other species, but they have a rather high degree of dissimilarity for two species in the same genus. The correlation shape analysis does not make the two closest neighbors. Most highly correlated with the large *M. albatus* is the large *Cheiromeles parvidens*; most highly correlated with the small *M. whitleyi* is the small *Molossops temminckii*. The correlation coefficient in both instances is low (0.501 and 0.566, respectively), and I suspect general size has affected which bats are neighbors. Likewise, I think the large distance (0.540) between the two species of *Myopterus* is also because of the size difference between the two bats and subsequent allometric changes that even the manipulation of the size-out analysis cannot eliminate. Increase in size has caused structural changes out of proportion with the smaller bat.

Myopterus joins *Molossops*, found only in the New World, at 0.690. The similarity between these Old and New World genera was noted by Miller (1907, p. 246) where he said, "This genus [*Myopterus*], immediately recognizable among Molossine bats by the peculiar form of the lower incisors, more closely re-

sembles the South American *Molossops* than it does any of the known Old World groups." At the time Miller was writing, the species of *Molossops* and *Cynomops* were both included in the genus *Molossops*, and he made an analogy between the large and small species of *Myopterus* and the large *Molossops cerastes* (=*Cynomops brachymeles*) and the small *Molossops temminckii*, the analogy being that the unusual size difference between the two species of *Myopterus* was not unique. My analysis, like Miller's, illustrates that species of great size difference can be closely related phenetically and interpreted as being in the same genus, as in *Myopterus*.

Although similar, I do not put species of *Myopterus* in the same genus with species of *Molossops* (*sensu lato*), but the relatively close morphological resemblance between these two groups is intriguing. *Myopterus*, a derived genus based on dental traits, has no living, close morphological neighbors in the Old World. I suspect *M. albatus* is the more derived of the two species of *Myopterus* because of its large size.

Myopterus has an unusual morphological character combination that should be mentioned. Most molossids with widely separated ears and unwrinkled lips, features characteristic of most *Mormopterus*-like and *Molossops*-like bats, have shallow basisphenoid pits. These features may indicate a feeding behavior fundamentally different from that of *Tadarida*-like bats. The two species of *Myopterus* have widely separated ears and unwrinkled lips, but they have deep basisphenoid pits, much like those in *Otomops*. I think this peculiar combination further distinguishes *Myopterus* as a distinct genus.

The closest phenetic relatives of *Myopterus*, size-out, are *Molossops temminckii*, then species of *Molossops* (*Cynomops*). I suspect these bats, *Myopterus*, *Molossops*, and *Cynomops*, had a common ancestor, and perhaps *Myopterus* could have had an origin in the New World. The only other African molossids with thick jaws and abbreviated dental pattern, and bats which I suspect eat hard-shelled items as *Myopterus* probably does, are species of *Mops*. It is possible that, with the proliferation of species of *Mops* into nearly all size categories, relatives of *Myopterus* were either squeezed out of existence or speciation in *Myopterus* never got started with the increased competition.

Only four species of *Eumops* make up the next group, but the other three species of that genus are phenetically related to these four and will also be discussed (fig. 22). The four in the immediate group are *E. bonariensis*, *E. underwoodi*, *E. glaucinus*, and *E. maurus*; the more distant forms are *E. hansae*, *E. perotis*, and *E. auripendulus*. Although scattered on the PCA, these seven bats do have a mutual resemblance (fig. 20). The four central species of *Eumops* and *E. hansae* are in the center of the PCA (fig. 4), whereas *perotis* is negative on axis II and *auripendulus* is positive on axis II. All seven bats have four lower incisors, but the posterior ridge on M^3 shows all stages of variability. Only six of the bats have a PM^3; and although the specimen of *E. maurus* I studied does not, other specimens of this bat from Suriname do have a small PM^3 (Eger, 1977). The lips of the seven *Eumops* have been coded as finely wrinkled and skirt-like, while the ears of all but *hansae* have been coded for the intermediate condition of joining in a V (this ear condition has definitely been miscoded for *E. perotis* which has well-joined ears). Basisphenoid pits are moderate to deep and wing tips are narrow to very narrow (table 11). The jaw structure and resulting food habits are variable. The large *E. underwoodi* and *E. auripendulus* are thought to

take hard-shelled items and the large *E. perotis*, soft ones. Nothing is known of the food habits of the four smaller species which have medium to thin jaws, but I suspect they take hard and soft items of appropriate size.

The relationship of *E. hansae*, *E. perotis*, and *E. auripendulus* to the four grouped *Eumops* is as follows (table 7): *E. hansae* is nearest *bonariensis* at a size-out distance of 0.690 but most highly correlated with *Tadarida aurispinosa* at 0.353; *E. perotis* is nearest *bonariensis* at a size-out distance of 0.702 and most highly correlated with *E. underwoodi* at 0.795 (surprisingly high); and *E. auripendulus* is nearest in size-out distance to *Molossus bondae* (0.523) but most highly correlated with *glaucinus* (0.714). The remaining four, the grouped species, are closest to one another in size-out and correlation but not always to the same congener (table 7).

Based on dental traits, *Eumops hansae* is probably a more primitive species of *Eumops* because it has a moderately developed PM³, metaconule on M¹, and a completely developed N-cusp pattern on M³, whereas *E. auripendulus* may be a more derived species with a small PM³ and a V-shaped pattern on M³. The other five bats cannot be graded as to primitive and derived dental traits. *Eumops perotis* bears a better developed PM³ than the others, but its M³ has the same degree of development (cusp less than one-half length of second cusp), whereas *E. bonariensis* has a better developed M³ (cusp more than one-half length of second cusp) but a small PM³. The remaining bats bear a small PM³ and a slight posterior cusp on M³ (PM³ in *E. maurus* is variable).

In the phenogram (fig. 22) *bonariensis* joins *underwoodi* at 0.480 and *glaucinus* joins *maurus* at 0.500. These two pairs unite at 0.610. Both *bonariensis* and *underwoodi* are most highly correlated with *perotis*, and while *glaucinus* is most correlated with *underwoodi*, *maurus* is most correlated with *glaucinus*. *Eumops maurus* is the only *Eumops* which has the same neighbor in both shape analyses. There is little or no historical support for these pairings. Sanborn (1932) reviewed the species of *Eumops* and mentioned that the skull of *bonariensis* was similar to that of *glaucinus*, and that *maurus* has a palate like that of *hansae* but is externally like *abrasus* (=*auripendulus*). He did think that *glaucinus* was the most nearly related species to *auripendulus*, a resemblance corresponding to my correlation analysis. Goodwin (1940) named *E. underwoodi* and noted that its skull was shorter and more robust than that of *E. perotis*, and that *underwoodi* really looked like a large *abrasus* (=*auripendulus*). Eger (1977) found, in her analysis using ratios (size is removed), both males and females of *auripendulus* and *underwoodi* paired up first and were then joined by *glaucinus*. Although our analyses are not exactly comparable (she looked at the genus only as an entity and analyzed males and females separately), *auripendulus*, *underwoodi*, and *glaucinus* are species of *Eumops* in my analysis with more robust jaws and skulls (fig. 4).

The more distant species of *Eumops*, except for *hansae*, are associated with other groups: *E. auripendulus* with *Molossus* and *E. perotis* with the *Tadarida-Otomops* complex. *Eumops hansae* is nearest *bonariensis* but correlated with *Nyctinomops aurispinosa*. Sanborn (1932) thought *hansae* was similar to *bonariensis* both in external appearance and in skull shape but that its teeth showed "a strong resemblance to *Tadarida* [including *Nyctinomops*]." When Miller (1902) named the genus *Nyctinomops*, he mentioned that it was intermediate between *Nyctinomus* (Old World *Tadarida*) and *Promops* (including *Eumops*). Drawings comparing the skulls of *hansae* and *aurispinosa* appear in Figures 20 and 15. My

study, as does Eger's (1977), shows *hansae* to be a distant and outlying member of the genus *Eumops*, and if tooth traits are taken into account and the fact that its ears are separated, it is the most primitive species in the genus.

I believe that *auripendulus* appears in the *Molossus* group because both *auripendulus* and *Molossus* have similar jaw and skull characteristics. Both have robust, heavily built skulls (figs. 20, 9). Besides skull characteristics, Brown (1967) found that the baculum of *auripendulus*, a stout rod-shaped bone, could be mistaken for the bacula in species of *Molossus*. As for general skull appearance, *auripendulus* looks more like other species of *Eumops* than like species of *Molossus* (fig. 20), but the fact that *auripendulus* has some of the characteristics of *Molossus*, such as the well-developed sagittal crest and thick dentary, cannot be doubted. I suggest that *E. auripendulus* is convergent with the genus *Molossus* rather than closely related to it phylogenetically.

Eumops perotis is nearest *E. bonariensis* (but at a great distance) and most correlated with *underwoodi* (at a rather high correlation). Other nearest neighbors include several species of *Tadarida* and *Nyctinomops*, with which *perotis* has several jaw and skull features in common. Actually *E. perotis* is a bat of unusually thin jaws for its size (see regressions in a previous section; fig. 7), and I suspect, it is an allometrically enlarged *Eumops* out of proportion with its smaller congeners. Although *perotis* has no baculum, *underwoodi* has one more similar in shape to that in *bonariensis* and *glaucinus* (Brown, 1967). The two large species of *Eumops*, however, do have the same chromosome number of 48 (Warner et al., 1974). In Figure 20 *E. perotis* appears as the largest of a series of similarly shaped species of *Eumops* and, I believe, is only convergent with the *Tadarida*-like genera with which it is associated in the phenogram.

This genus, ironically called *Eumops*, "true molossid," is the most difficult to describe as a particular shape because of its great variation. Historically, species of *Eumops* have been placed in several other genera including *Promops*, *Molossus*, *Myopterus*, and *Tadarida*. My study is no exception in not clearly grouping all the classical species of *Eumops* into one cluster. Because several species are allied morphologically with other clusters, one may wonder if there is a typical *Eumops*-like shape and whether the genus is monophyletic or polyphyletic. I think that species of *Eumops* are monophyletic because of their phenetic similarity in the clustering analyses, their sharing of several derived traits, and their similarity of skull shape. Several forms, however, are convergent toward other ways of molossid life. These convergent forms are the larger species in the genus.

The chromosome work by Warner et al. (1974) and by Dulic & Mutere (1973) presented data on 24 species of molossids. Of these 24, 20 were found to have 48 chromosomes. In the four species of *Eumops* analyzed, *underwoodi* and *perotis* have 48, *auripendulus* has 42, and *glaucinus* has either 40 or 38 (in Colombia and in Chiapas and Costa Rica, respectively). Authors of both papers suggest that 48 is the primitive number of chromosomes for Molossidae. This notion of primitive chromosome number is only partially correlated with the tooth loss configuration in *Eumops*. *Eumops auripendulus* has not only the most derived teeth but also a derived chromosome state. *Eumops glaucinus*, on the other hand, though it has a lower chromosome number, has dental characteristics which are neither derived nor primitive. This last species is grouped with three other species of *Eumops* which make up the cluster of more typical species.

Two species in the distinctive genus *Promops* follow the four species of

Eumops in the phenogram (fig. 20). These two bats are positive on axis II of the PCA (fig. 4), but are not as extreme as *Molossus*. The skull of *Promops*, although shorter and rounder than that of *Molossus*, is not as robust nor is its dentary as thick (fig. 10). Sometimes called the domed-palate bats, species of *Promops* have a distinctive, highly arched palate. These two species have four lower incisors, vestigial PM³, and reduced M³ that has no posterior cusp. Wing tips are narrow, ears join in a V-pattern, lips are unwrinkled, palate is not emarginated, and basisphenoid pits are developed (table 11).

The larger *P. centralis* joins the smaller *P. nasutus* at 0.310. The two are closest neighbors in both shape analyses. *Promops* joins *Eumops* at 0.690. Although the nearest neighbor of both species of *Promops* is a species of *Molossus*, the average distance to the seven species of *Molossus* is greater than the average to the four species of *Eumops*, hence the clustering of *Promops* with the group of four *Eumops*. Most highly correlated neighbors are also *Molossus*. Other authors have remarked on the similarity of *Promops* to *Eumops* and *Molossus*. Miller (1907) stated that *Promops* was intermediate between *Eumops* and *Molossus* but closer to *Molossus*. In dental features, *Promops* does appear intermediate; but in skull features, it is more similar to *Molossus*. Brown (1967) noted that *Promops* has no baculum as is the case in *E. perotis*, but all four species of *Molossus* he examined had at least a small one. *Promops* is also related phenetically to *Molossops temminckii* (size-out distance is 0.704). The two genera, *Promops* and *Molossops*, have several traits in common including relatively thick jaws, unemarginated palate, and unwrinkled lips.

The genus *Molossus* and *Eumops auripendulus* make up the final large cluster of molossids. Because *auripendulus* has already been examined, this discussion concerns itself primarily with traits and relationships of species of *Molossus*. *Molossus* represents an extreme morphological condition for molossids. These bats have thick jaws, well-developed cranial crests, fewer teeth and cusps, and very narrow wing tips (fig. 9, table 6). They are the most positive on axes II and IV and most negative on III in the PCA (fig. 4). There is evidence that species of *Molossus* eat hard-shelled items, such as beetles. All species of *Molossus* have a V-shaped cusp pattern on M³ and have lost PM³ and I₂. They have also nearly lost the lower third premolar, a tooth which is probably being squeezed out by the lower canine and PM₄. All species of *Molossus* have basisphenoid pits, slightly joined ears, unwrinkled lips, and no palatal emargination (table 11).

Skulls of different species of *Molossus* are difficult to distinguish except for size (fig. 9). Quantitative proof of their similarity can be noted by the fact that five of the species group together before the 0.420 average-least-distance line in Figure 22 and by the high correlation values among all the species (table 7). Although care was taken to use only specimens of distinct species, there may still be misnamed specimens. No recent study has been done which clearly demarcates the species of *Molossus*. The grouping here includes seven OTU's based on 76 measurements and may not agree with the notions of previous authors.

Molossus sinaloae and *M. molossus* form a pair at 0.290. Each is the other's nearest neighbor (table 7), but while *sinaloae* is most highly correlated with *molossus*, the latter is most correlated with *bondae*. It is true that *molossus* and *bondae* are more nearly the same size and *sinaloae* is larger. Hall & Kelson (1959, p. 216) mentioned *M. bondae* as "purportedly resembling *Molossus sinaloae* but smaller," a note which my analysis does not support.

Molossus ater, the largest *Molossus,* joins the *sinaloae-molossus* pair at 0.340. The nearest neighbor to *ater* in both shape analyses is *sinaloae.* In the past (Miller, 1913) the larger species of *Molossus,* such as *ater, sinaloae,* and *pretiosus,* have been put into a group separate from the groups of smaller species; but more recently (Jones et al., 1971; D. C. Carter, personal communication) groupings of species of *Molossus* have been suggested based on the length and color of the hair. There are two types of hair, long and bicolored (white at base) or short and unicolored (black at base). This analysis does not agree with those groupings based on hair: *M. ater* has short, unicolored hair, while *M. sinaloae* and *M. molossus* have long, bicolored hair. The latter two are, of course, paired (fig. 22).

Molossus bondae and *M. coibensis* pair at 0.250, the lowest distance of any two bats in the study and may represent the same species. These two are also most highly correlated with each other. Historically, the small *M. coibensis* has been thought of as a subspecies of *M. molossus* (Hall & Kelson, 1959; K. F. Koopman, personal communication), and both have long bicolored hair, but the two are not grouped together here. At 0.390 the *bondae-coibensis* pair joins *ater, molossus,* and *sinaloae.* These five are similar morphologically despite the variation in size. It is a cluster which includes both the largest (*ater*) and the smallest (*coibensis*) species of *Molossus.*

Molossus trinitatus joins the main cluster of species of *Molossus* at 0.470. It is nearest *bondae* in the size-out analysis but more correlated with *sinaloae.* Ojasti & Linares (1971) suggested that *trinitatus* is a subspecies of *sinaloae.* Goodwin (1959), however, noted that this rare bat is not really close to any other *Molossus* but it does have the same long, bicolored hair as *sinaloae.* Brown (1967) reported that the baculum of *M. trinitatus* is longer than that of *sinaloae* and more pointed than that in any other species of *Molossus* he examined. In this analysis *M. trinitatus* is less robust than the other species of *Molossus* in several jaw and skull features and is the species of *Molossus* which is closest to the species of *Promops* in morphology. In my study, I am hesitant to call *trinitatus* a subspecies of any other species of *Molossus.*

The last *Molossus, M. pretiosus* joins the cluster at 0.570. In both shape analyses it is closest to *ater,* another large bat. Why *pretiosus* joins at a greater distance is uncertain, but it appears to be distinct from other *Molossus.* Although like *M. ater* in having short, unicolored hair, I agree with Jones et al. (1971) that *M. pretiosus* is not conspecific with *ater* as was stated by Handley (1966).

In my earlier, larger analysis several smaller but questionable species were included as OTU's: *M. barnesi, M. lambi,* and *M. pygmaeus.* These three placed sufficiently close to *M. molossus* that I omitted them from my analysis and used only *M. molossus* to represent that particular species. There are no less than eight named, chiefly insular forms originally described as separate species distinct from *M. molossus.* Now most of the forms, both island and mainland, are considered to be synonyms or subspecies of *M. molossus* (see Koopman, 1968; Husson, 1962; Jones et al., 1971).

Two vespertilionid bats, *Nyctalus* and *Mimetillus,* are included in my study to see how close, phenetically, they are to molossids (fig. 22). I chose these two for being molossid-like and not for being typical vespertilionids. Although the phenogram is not as good at representing great distances as it is with smaller ones, it is interesting to note that these two bats appear more phenetically

similar to the main body (they average closer) of molossids than does the genus *Cheiromeles*. *Nyctalus* and *Mimetillus* are each other's nearest neighbor (size-out), but as vespertilionids, they are phenetically closer to the *Mormopterus*-like molossids than to any other group (table 9). Vespertilionids are generally thought of as more primitive than molossids and the similarity of these two species with some of the more primitive molossids is not unexpected. These two do have widely separated ears, no wrinkles, wide anterior palatal emargination, and well-developed M³s.

Cheiromeles is the most distinctive genus, morphologically, in the family (fig. 22). The two species are extremely robust molossids with a large body, thick dentaries, wide face and widely separated, short, erect ears, unwrinkled lips, no basisphenoid pits, and broad wing tips. In the PCA *Cheiromeles* occupies a position on the extreme positive end of axes II and III, but it is only slightly negative on axis IV (fig. 4). I suspect that species of *Cheiromeles* eat hard-shelled prey.

Based on tooth reduction, *Cheiromeles* is more derived than *Molossus* because of its functionless PM3. Although small in *Molossus*, this tooth is vestigial in *Cheiromeles*. The two genera are most likely similar because of convergent food habits and not because of a close common ancestor. The molossid to which both species of *Cheiromeles* appear phenetically related in the size-out analysis is *Molossops temminckii*, but the two are most highly correlated with *Cynomops brachymeles*. There is some similarity in the shape of the skulls (figs. 17, 19) of these species as well as in the external appearance of the head (widely separated, short, erect ears and unwrinkled lips). Perhaps the *Molossops-Cynomops* ancestor mentioned earlier not only started a line that ends in *Myopterus* in Africa but also a line that ends in *Cheiromeles* in the Indo-Malayan region.

Generic Considerations

At or before 0.600 in Figure 22, nine genera form. They are *Nyctinomops* (New World *Tadarida*), *Otomops*, *Chaerephon*, *Mops*, *Molossops*, *Myopterus*, *Promops*, *Molossus*, and *Cheiromeles*. Only *Tadarida*, *Mormopterus*, and *Eumops* do not. The morphological distance or dispersion among species within these three genera is greater than that in the other nine. Also complicating matters is that the method which clusters the species for the phenogram, unweighted pair-group method using arithmetic averages (UPMGA), does not always group OTU's next to its nearest neighbor. Each juncture must be checked in the size-out distance matrix from which the phenogram was taken to see if each OTU has been placed next to or near its nearest neighbor. I believe that 12 natural groups can be discerned in the family because of phenetic similarity, despite the relatively great dispersion in three of the groups.

Specifically, I restrict the genus *Tadarida* to seven Old World and one New World species: *T. teniotis*, *T. africana*, *T. fulminans*, *T. lobata*, *T. australis*, *T. kuboriensis*, *T. aegyptiaca*, and *T. brasiliensis*. The last two are smaller and form a connection with New World molossids. Although all these species of *Tadarida* join together at 0.690 (*T. aegyptiaca* and *T. brasiliensis* average juncture to the group is 0.570), I think they are too similar to be split any further. These eight species form one of the most morphologically dispersed molossid genera.

Species of the genus *Nyctinomops* (formerly species of *Tadarida* from the New World) form a distinct cluster at 0.570 and include *N. aurispinosa*, *N.*

femorosacca, N. laticaudata, and *N. macrotis.* Although *Nyctinomops* and *Tadarida* are phenetically similar, there is no one bat that forms a specific connection, not even *T. brasiliensis,* the only species of *Tadarida* in the New World.

Species of *Otomops* form a cluster just before the arbitrary line: *O. martiensseni, O. secundus, O. wroughtoni,* and *O. papuensis.* These species have the distinctive *Otomops* shape whether large or small. *Otomops* is phenetically related to *Tadarida* through *T. teniotis.*

Species of *Chaerephon* are restricted to medium-sized, *Tadarida*-like bats and form a cluster before the arbitrary line at 0.540. The genus includes *C. ansorgei, C. bivitatta, C. aloysiisabaudiae, C. russata, C. major, C. nigeriae, C. pumila, C. chapini, C. bemmelini, C. plicata,* and *C. johorensis.* With some inconsistency, I add *C. jobensis* to species of *Chaerephon,* and though both shape neighbors are species of *Mops,* it has teeth like those of *Chaerephon.* Until a study with more than one specimen is done I think *jobensis* should remain in *Chaerephon. Chaerephon* and *Tadarida* are phenetically related through *C. ansorgei, C. bivitatta,* and *C. bemmelini.*

Species of *Mops* form a cluster at 0.570 and consist of small, medium-sized, and large bats, including *M. condylura, M. brachyptera, M. thersites, M. trevori, M. niangarae, M. congica, M. demonstrator, M. niveiventer, M. midas, M. leonis, M. nanula, M. spurrelli, M. mops,* and *M. sarasinorum.* There is a phenetic relationship between *Chaerephon* and *Mops* through *M. condylura* and possibly *C. jobensis.*

Species of the genus *Mormopterus* are more dispersed relatively than most other genera and include the New World *M. (Mormopterus) kalinowskii, M. (Mormopterus) minutus,* and *M. (Mormopterus) phrudus;* the Australasian *M. (Mormopterus) loriae, M. (Mormopterus) norfolkensis, M. (Mormopterus) planiceps,* and *M. (Mormopterus) beccarii;* the African-Malagasy *M. (Mormopterus) jugularis* and *M. (Mormopterus) acetabulosus;* and the African *M. (Sauromys) petrophilus* and *M. (Platymops) setiger.* Some of the morphological dispersion in this genus occurs because I have included *Platymops* in the genus. Although I prefer to lump *Platymops* (distance to nearest neighbor, *Mormopterus acetabulosus,* is 0.673) with species of *Mormopterus,* probably a case could be made to leave it as a monotypic genus. *Mormopterus* is phenetically related to *Tadarida* through *T. brasiliensis* and *T. aegyptiaca* and to several *Molossops*-like bats especially *Molossops (Neoplatymops).*

Molossops, like *Mormopterus,* includes bats with a variety of tooth configurations, but all are phenetically similar to *Molossops. Molossops* includes *M. (Molossops) temminckii, M. (Neoplatymops) mattogrossensis, M. (Cynomops) brachymeles, M. (Cynomops) planirostris,* and *M. (Cynomops) greenhalli.* These bats form a group at 0.610. *Molossops* joins *Myopterus* at 0.690, an Old World genus with which *Molossops* shares many morphological features.

The two species of *Myopterus, M. albatus* and *M. whitleyi,* although like *Molossops,* are distinctive in dental configuration and in the great development of the basisphenoid pits, but the two genera are phenetically related. *Myopterus* is one of the most derived molossid genera and is the most derived of the Ethiopian molossids.

Species of *Eumops,* although a few have some morphological resemblance to other genera, are I think, more similar to one another than to any other group. This genus includes *E. hansae, E. bonariensis, E. underwoodi, E. glaucinus, E. maurus, E. perotis,* and *E. auripendulus.* There is a phenetic relationship between

Nyctinomops and *Eumops* through *N. aurispinosa* and *E. hansae. Eumops* is another of the more morphologically dispersed genera in the family.

The genus *Promops* includes two species, *P. nasutus* and *P. centralis,* and seems intermediate between *Eumops* and *Molossus* phenetically. Although *Promops* is similar to several species of *Eumops,* the genus does have some resemblance with species of *Molossops.*

Bats of the genus *Molossus* form a distinct cluster before the arbitrary line at 0.570 and include *M. ater, M. molossus, M. sinaloae, M. bondae, M. coibensis, M. trinitatus,* and *M. pretiosus.* These bats are phenetically related to *Promops* through *M. trinitatus.*

Cheiromeles, like *Myopterus,* is phenetically related to *Molossops* in the New World. As large bats, the two species in the genus are greatly out of proportion with any other similar, but smaller, molossid bats. *Cheiromeles* has the most derived dental configuration of any genus in the family.

Even though several of the nine primitive-derived characters (table 11) used to help determine the phyletic relationships have been used in the past by several students of molossid taxonomy (Hill, 1961; Rosevear, 1965; Hayman & Hill, 1971; Peterson, 1965, 1967, 1969, 1971a,b, 1972, 1974; Koopman, 1975), these characters could still be plastic because of functional morphology. Already eliminated are characters related to the development of the sagittal and lambdoidal crests because changes can be seen not only between males and females of a species but also between young and old animals. Characters such as tooth loss, separated ears, lack of basisphenoid pits, unwrinkled lips, and closed palatal emargination, however, may be related to eating beetles and may not be good phylogenetic characters to use. Likewise, the narrowness of a wing tip may have more to do with where a bat lives than to which bat it is related. In other words, many of the nine characters may not be conservative enough to indicate patterns of molossid phylogeny. In Figure 24 I show the cladistic relationships based on only four of the primitive-derived characters: ears, basisphenoid pits, palate, and wrinkles. These four may be less plastic than the other characters concerned with loss of bone or dental material. A summary of all nine characteristics for each genus also appears in Figure 24. I do not think the cladogram gives the whole picture, however, and based on what is now known from the phenetic data, I believe I can present a more complete phylogenetic picture.

Basically, there are two kinds of molossids: those with widely separated ears and those with joined ears. The first dichotomy in the cladogram separates these two groups. The bats with widely separated, short, erect ears usually have shallow or no basisphenoid pits and little or no development of wrinkles on the lips. These bats I call *Mormopterus*-like bats and include *Mormopterus* (with *Sauromys* and *Platymops*), *Molossops* (with *Cynomops* and *Neoplatymops*), *Cheiromeles,* and *Myopterus.*

Mormopterus itself is a genus that has the fewest derived traits. No one species of *Mormopterus* has all the primitive characteristics. Several of these bats do have six lower incisors, the maximum number for chiropterans. In my study it is *Mormopterus* that has a closer phenetic similarity to vespertilionids than any other genus.

Molossops, Cheiromeles, and *Myopterus* are separated from *Mormopterus* (fig. 24) because they have no anterior palatal emargination and no wrinkles on the

lips (species of *Mormopterus* are variable in this last trait). Finally, *Myopterus* at the end of this branch is separated from *Molossops* and *Cheiromeles* by having well-developed basisphenoid pits.

As for the more variable primitive-derived traits, all species of *Molossops* have lost I3 and the metaconule on M¹; *Molossops* (*Molossops*) has lost I2. All but *M.* (*Neoplatymops*) have lost PM³ and much of the posterior commissure on M³; and the three species of *M.* (*Cynomops*) have narrow wing tips. Phenetically, the more primitive *M.* (*Neoplatymops*) has characteristics that are similar to both *Molossops* and *Mormopterus*.

Character		Mormopterus	Molossops	Cheiromeles	Myopterus	Tadarida	Chaerephon	Mops	Otomops	Nyctinomops	Eumops	Promops	Molossus
9	M³	-	(+)	+	+	-	-	+	-	-	(+)	+	+
8	M¹	-	+	+	+	-	(+)	+	+	+	+	+	+
7	PM³	(+)	(+)	+	+	-	-	-	-	-	-	-	+
6	INCISORS	(4)	(4)	2	2	(4)	4	4	4	4	4	4	2
5	WING	-	(+)	-	-	(+)	-	-	-	+	+	+	+
4	WRINKLES	(+)	-	-	-	+	+	+	+	+	+	-	-
3	PALATE	-	+	+	+	-	-	-	-	-	+	+	+
2	PITS	-	-	-	+	(+)	(+)	(+)	+	(+)	+	+	+
1	EAR	-	-	-	-	(+)	+	+	+	+	(+)	+	+

FIG. 24. Summary and cladogram of primitive (−) and derived (+) traits for genera of molossid bats. When a genus has species with both states, the symbol is circled. Traits for each species are listed in Table 11. The cladogram is aligned with the columns in the table. A line is drawn after the first four characters on which the cladogram is based (see text for explanation).

Like *Molossops, Cheiromeles* and *Myopterus* have both lost teeth so that each has the most derived molossid dental formula. Data from my phenetic study suggest that *Myopterus* and *Cheiromeles* are related to *Molossops*.

The bats remaining on the right-hand branch of the cladogram (fig. 24) are bats with large, slouched ears, well joined over the nose or ears intermediate in size and just joining over the nose and some development of the basisphenoid pits. These, I think, are *Tadarida*-related molossids and include *Tadarida* (both hemispheres), *Chaerephon, Mops,* and *Otomops* in the Old World; and *Nyctinomops, Eumops, Promops,* and *Molossus* in the New World.

Tadarida, like *Mormopterus,* has species with few derived characters and two species, *Tadarida teniotis* and *T. brasiliensis,* have the greatest number of teeth (32) of all molossids (but not the maximum for Chiroptera, which is 38). A close phylogenetic relationship may exist between *Tadarida* and *Mormopterus* because *T. brasiliensis* and *T. aegyptiaca* have been placed close to species of *Mormopterus* phenetically (fig. 22).

In the four more conservative characters from which the cladogram was composed, *Tadarida, Chaerephon, Mops, Otomops,* and *Nyctinomops* share the same derived traits, namely large, slouched ears joined over the nose, development of the basisphenoid pits (though this is a variable trait among species), and wrinkled lips. There are some differences, however, in the more variable traits. With *Chaerephon* and *Mops* there is change in the toothrow toward a more derived state, particularly in *Mops,* and several species of both genera have a palatal emargination that is nearly closed. Neither *Chaerephon* nor *Mops* have species with narrow wing tips as do some species of *Tadarida. Otomops* and *Nyctinomops* share many of the same derived characters with *Tadarida,* but the characters seem to be amplified. All species of *Otomops* have deep basisphenoid pits and all species of *Nyctinomops* have very narrow wing tips. The phenetic data suggest possible phylogenetic relationships between *Tadarida* and *Chaerephon* and between *Chaerephon* and *Mops,* between *Tadarida* and *Otomops,* and between *Tadarida* and *Nyctinomops.*

The next genus, *Eumops,* has, for the most part, the derived condition for all four of the less variable traits in Figure 24. Nearly all the species of *Eumops* have joined ears, basisphenoid pits, closed anterior palate, and fine wrinkles on the lips (*E. hansae* is coded for having separated ears). Just past *Eumops* in the cladogram are *Promops* and *Molossus,* genera which I think have had a reversal in the wrinkles on their lips. These three genera, *Eumops, Promops,* and *Molossus,* are more derived than *Tadarida* because they all have narrow wing tips and some abbreviation of the teeth (*E. hansae* is the only exception). The three have more derived characters than any of the other molossid genera, and *Molossus* has the most derived toothrow of any *Tadarida*-related genus. The phenetic data suggest *Eumops* has some relationship to *Nyctinomops,* and *Molossus* is closely related to *Promops.* Although I am less sure about the phylogenetic relationship between *Promops* and *Molossus* with other molossid genera, *Promops,* after *Molossus,* is phenetically nearer four species of *Eumops* and next closest to species of *Molossops.* Cladistically, the ears, although shorter, are more like those of *Eumops* and other *Tadarida*-related bats rather than those of *Molossops;* hence the placement of *Promops* in the cladogram.

In conclusion, I think there are two major groups of molossids based on ear design. Within each group, parallel trends occur which are probably related to

two basically different methods of detecting and consuming prey. Within the *Mormopterus* groups there are bats that have gracile skulls and jaws with the more primitive toothrow configuration (*Mormopterus* [*Mormopterus*], *Molossops* [*Neoplatymops*]) and bats with robust skulls and jaws that tend to lose teeth (*Molossops* [*Cynomops*], *Myopterus*, *Cheiromeles*). Likewise, in the *Tadarida* groups, *Tadarida*, *Chaerephon*, *Otomops*, *Nyctinomops*, and some species of *Eumops* have less robust skulls and *Mops*, *Eumops* (part), *Promops*, and *Molossus* have more robust skulls and some abbreviation of the toothrow.

Geographic Considerations

Is there any pattern to how molossids diversified morphologically in different areas? What is the composition of each fauna in terms of primitive and derived molossids? What fauna might be the oldest?

This last section is an extension of the Ecology section in that I infer the ecological structure of each molossid fauna from the morphological structure. For this reason, the distance values used here include the size of the bats. Findley (1975) has done a similar study but of a total bat community.

A simple way to look at the morphological dispersion of a fauna, statistically, is to determine each bat's average distance ($\bar{d}$) to every other bat in that fauna, to sum the averages, and to take the faunal average ($\bar{\bar{d}}$). The average distance for each bat tells how close an individual bat is from every other bat in the particular fauna (see Findley, 1975). A low average indicates that the bat is phenetically similar to most of the bats in the fauna, and a high $\bar{d}$ value indicates that the bat is more distinct phenetically (more unusual morphologically) and is farther away from other members of the fauna. In detecting the highly distinctive taxa in each fauna, I can give some idea of which bats are affecting the morphological dispersion; and by calculating the $\bar{\bar{d}}$ for each fauna, I can compare the dispersions in each fauna.

The bats in all three faunas and their average distance to their faunal neighbors are listed in Table 12. By the Kruskal-Wallis nonparametric test, a very significant difference ($p < .001$) occurs among the $\bar{d}$ values of the three faunas, but exactly which faunas are significantly different presents a statistical problem. Because there is no nonparametric multiple range test to handle unequal sample sizes, a Mann-Whitney U test was run on all combinations of two of the three faunas. The Indo-Australian fauna is more dispersed than the Ethiopian and the Neotropical faunas at very significant levels ($p = .0001$ and $p = .0004$, respectively). The Neotropical fauna is more dispersed than the Ethiopian fauna but at a lower level of significance ($p = .0238$).

The distributions of the averages in each fauna are shown in Figure 25. Ethiopia contains several bats with relatively low $\bar{d}$ values, lower than in either of the other two faunas, and several bats with only moderately high values, like *Otomops martiensseni*, *Mops midas*, and *Tadarida africana*. The bats in this fauna are the least dispersed of the three and have the least morphologically distinctive molossids.

Molossids in the Neotropical fauna have no members with averages as low as those in the Ethiopian and contain two bats with averages higher than the highest ones in Ethiopia. This second fauna is not only more dispersed statistically than the first, but it also contains the distinctly different molossids, *Eumops perotis* and *E. underwoodi*.

TABLE 12. Average distance ($\bar{d}$) of each molossid bat to every other bat in its respective fauna. The means for each fauna ($\bar{\bar{d}}$) are significantly different by a Kruskal-Wallis non-parametric test ($p = .000001$). More specifically, the Mann-Whitney U test shows that the Indo-Australian fauna is significantly different from the Ethiopian ($p = .0001$) and Neotropical ($p = .0004$) faunas; and the Neotropical fauna is significantly different from the Ethiopian fauna ($p = .0238$).

Ethiopia	$\bar{d}$	Neotropics	$\bar{d}$	Indo-Australia	$\bar{d}$
T AEGYPA	.986	T AURISA	1.130	T TENIOA	1.375
T AFRICA	1.435	T BRASIA	1.196	T AUSTRA	1.422
T FULMIN	1.110	T FEMORA	1.171	T KUBORI	1.304
T LOBATA	1.173	T LATICA	1.055	TC JOHOR	1.229
T ANSORA	.884	T MACROA	1.372	TC PLICA	1.219
TC ALOYA	.927	TR KALIN	1.294	TC JOBEN	1.248
TC BIVIA	.868	TR MINUA	1.432	TM MOPSA	1.215
TC BEMMI	.928	TR PHRUD	1.205	TM SARSA	1.290
TC CHAPI	1.221	E AURIPA	1.411	TR BECCR	1.459
TC MAJOR	.904	E BONARA	1.009	TR LORIA	1.599
TC NIGEA	.894	E GLAUCA	1.354	TR NORFA	1.491
TC PUMIA	.925	E HANSAE	1.151	TR PLANA	1.498
TC RUSSA	1.017	E MAURUS	1.058	OTO PAPU	1.306
TM BRACH	.941	E PEROTA	2.280	OTO SECA	1.366
TM CONDA	.996	E UNDERA	2.035	OTO WROA	1.443
TM CONGA	1.377	MP TEMMA	1.367	C PARVID	2.826
TM DEMOA	.939	CP BRACA	1.180	C TORQUT	2.747
TM LEONA	.999	CP GREEA	1.074		
TM MIDAA	1.652	CP PLANA	1.176	$\bar{\bar{d}}$	1.532**
TM NANUA	1.201	NEOPLATA	1.379	s	.471
TM NIANG	1.182	M ATERA	1.196		
TM NIVEI	.962	M BONDAA	1.020		
TM THERA	.952	M COIBEA	1.168		
TM TREVO	1.172	M MOLOSS	1.096		
XIPHONYC	1.288	M PRETIA	1.205		
TR ACETA	1.336	M SINALA	1.043		
TR JUGUA	1.150	M TRINIT	1.014		
MYOP ALB	1.353	PRO CENA	1.062		
MYOP WHA	1.129	PRO NASU	1.042		
OTO MARA	1.606				
PLATYMOP	1.262	$\bar{\bar{d}}$	1.247*		
SAUROMYS	1.092	s	.280		
$\bar{\bar{d}}$	1.121				
s	.207				

130
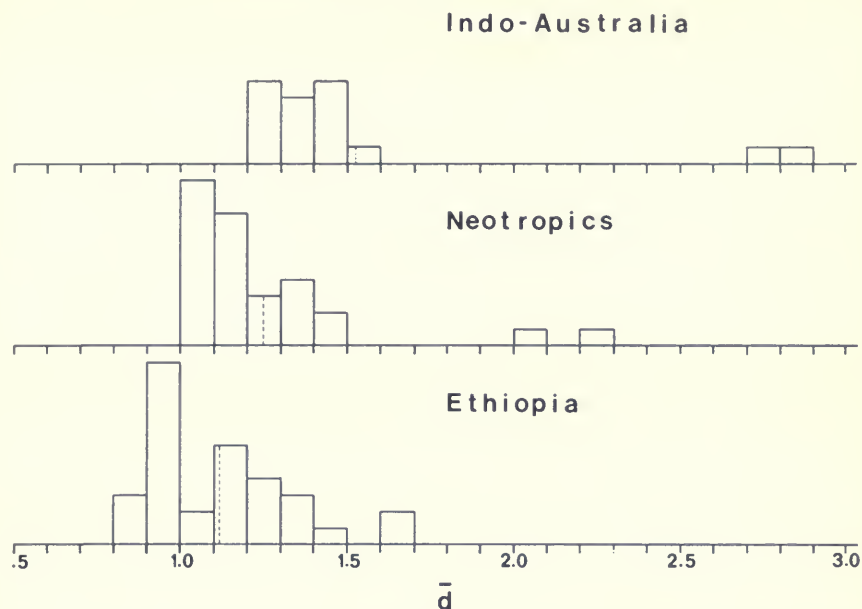
FIG. 25. Distribution of average distances ($\bar{d}$) in three molossid faunas. The dashed line in each figure represents the mean value ($\bar{\bar{d}}$) for that fauna. A list of $\bar{d}$ values is given in Table 12.

The third fauna, the Indo-Australian, contains molossids even more dispersed than those in the Neotropics and has the most highly distinctive taxa of any molossid fauna, namely *Cheiromeles parvidens* and *C. torquatus*.

Findley (1972, 1975) reasoned that the more phenetically diverse a fauna, the older it is; hence, in this analysis the Indo-Australian fauna would be the oldest; the Neotropical, next oldest; and the Ethiopian, the youngest. Probably a good case can be made for this arrangement, including the idea that *Cheiromeles* is the remnant of an ancient molossid fauna. The Indo-Australian fauna is depauperate of molossid species compared to the other two faunas. Coincidentally, and perhaps importantly, two species of echolocating swiftlets (*Collocalia*) occur in this region, and Fenton (1975) suggested that possible competition with these birds helped to make or keep the fauna depauperate of molossids. If so, maybe the presence of the birds helped to disperse the molossid fauna morphologically as well.

A second case can be made for the oldest molossid fauna being the Ethiopian. This fauna contains the greatest concentration of molossids which are most similar phenetically and the least dispersed of the three faunas. Not only have more species evolved in the Ethiopian fauna, but they have also radiated into more ecological roles (table 10). There are presently both small and very large moth eaters and small and very large beetle eaters, roles filled by ecologically diverse but relatively primitive molossids. The majority of species are *Tadarida*-related bats. The Indo-Australian and Neotropical faunas are more diverse phenetically, but the first lacks a very large moth-eater and the second, a very large beetle-eater. I think the very large bats in each of these faunas repre-

sent examples of ecological release into unique niches where no competition has occurred for some time.

Still a third case can be made for the Neotropical region having the oldest fauna because it has the most derived genera, *Eumops, Promops,* and *Molossus;* based on the nine primitive-derived traits. Among these derived genera are species specialized for moth diets and species specialized for beetle diets. Also the Ethiopian *Myopterus* and the Indo-Australian *Cheiromeles* are phenetically related to *Molossops* in the New World; *Tadarida aegyptiaca* and *T. brasiliensis* are related and *T. brasiliensis* may be the most primitive living molossid; and the more derived species of *Mormopterus* are in the New World while their close phenetic neighbors are in both Ethiopia and Indo-Australia. This fauna of the New World contains a large concentration of *Mormopterus-*related bats.

SUMMARY

The primary goal of my study, determining natural morphological groups of molossid bats, is accomplished by defining exactly the variation which occurs among the extant molossid species. I attempted to include as many of the species in the family as was possible.

To do this, I used principal components, distance (size-in and size-out), and correlation analyses on 80 species. Morphological trends that emerge from the data are size, as indicated by the first component; a suite of jaw characters, by the second; several facial features, by the third; and a few less important features, but particularly a wing characteristic, by the fourth. Each of the groups of phenetically similar molossids which appear in the PCA and in the distance and correlation analyses are described in terms of characters which are most highly correlated with the components. In particular, the second component, concerned with jaw structure, divides the species in the following way: *Cheiromeles, Molossus, Promops, Mops, Myopterus, Molossops* (including *Neoplatymops* and *Cynomops*), and several species of *Mormopterus* (including *Platymops*) and *Eumops* are located on the positive side of this axis, meaning these molossids have relatively thick jaws and robust skulls; molossids on the negative side, *Tadarida, Nyctinomops, Chaerephon, Otomops,* and several species of *Mormopterus* (including *Sauromys*) and *Eumops,* have thin jaws and less robust skulls. I use the suite of jaw characters to predict what molossids are eating and give data to support the predictions: bats with thick jaws eat hardshelled insects like beetles, and bats with thin jaws eat soft-shelled insects like moths. Likewise, I predict where molossids may be roosting or flying based on the shape of their wing tips. Bats with broad (relative to other molossids) wing tips may be slower and more maneuverable than molossids with narrow tips, and the few data available support this notion. Molossids tend to have two kinds of appearances: one with large, anteriorly directed ears which are joined over the nose, lips that are wrinkled, and basisphenoid pits that are medium or deep; and the other with short, laterally directed ears which are widely separated, lips that are unwrinkled, and basisphenoid pits that are shallow or nonexistent. I suspect that the two different appearances indicate two different ways in which molossids detect and consume prey, but I have no data to support or refute this thought.

Ecologically, both New and Old Worlds contain molossids with thick and thin jaws, *Molossus* in the New World and *Mops* in the Old World are probably

ecological counterparts in that both probably concentrate on hard-shelled foods. The same is true of several molossids with thin jaws in both the New and Old Worlds; these bats are probably concentrating on soft-shelled prey. However, in another morphological characteristic, the width of the wing tip, the fauna in the New World contains most of the species with narrow wing tips. As for general size in molossids, the percentage of medium-sized bats is approximately the same in both New and Old Worlds; but the Old World tends to have a greater percentage of large molossids, whereas the New World has a greater percentage of small ones.

The evolutionary or phylogenetic relationships among the species and the genera are examined phenetically and with the use of several primitive-derived characters. Twelve genera are delineated:

Chaerephon (formerly *Tadarida* [*Chaerephon*])
Cheiromeles
Eumops
Molossops (including *Neoplatymops* and *Cynomops* as subgenera)
Molossus
Mops (formerly *Tadarida* [*Mops*]; includes *Xiphonycteris*)
Mormopterus (formerly *Tadarida* [*Mormopterus*]; including *Sauromys* and *Platymops* as subgenera)
Myopterus
Nyctinomops (including four New World species formerly assigned to *Tadarida*)
Otomops
Promops
Tadarida

Three of these genera, *Tadarida*, *Mormopterus*, and *Eumops*, are more dispersed morphologically than the other nine. I think all 12 form natural groups based on morphological similarity.

In terms of primitive-derived traits, two groups emerge: the *Mormopterus*-like bats and the *Tadarida*-like bats. *Tadarida* and *Mormopterus* are the two most primitive genera to which all other genera can be related. The two groups differ primarily in ear design, separated or joined, and associated characters mentioned above and represent two basically different ways of detecting and consuming prey. Parallel trends of tooth loss and increased robustness of the skull occur in both groups. Genera in the *Mormopterus* group are *Mormopterus*, *Molossops*, *Myopterus*, and *Cheiromeles*; and genera in the *Tadarida* group are *Tadarida*, *Nyctinomops*, *Chaerephon*, *Mops*, *Otomops*, *Eumops*, *Promops*, and *Molossus*. These last three genera are the most derived in the family.

Geographically, the Indo-Australian molossid fauna is the most dispersed morphologically followed by the Neotropical and Ethiopian faunas. Good cases can be made for all three being the oldest molossid fauna: morphologically, the most distinctive genus, *Cheiromeles*, is found in the Indo-Australian fauna; ecologically, the Ethiopian molossids seem to fill more completely the available niches; and phylogenetically, the most derived genera are in the New World.

APPENDIX A

Data for 76 characters for each of 80 OTU's. Abbreviations are in Materials and Methods section.

	T AEGYPA	T AFRICA	T ANSORA	T AURISA	T AUSTRA	T BRASIA	T FEMORA	T FULMIN	T KUBCRI	T LATICA
HEAD BOD	74.000	104.500	74.000	74.000	84.000	67.000	62.000	84.000	89.000	66.000
TAIL	44.000	61.500	34.000	41.000	48.000	37.000	44.000	51.000	41.000	38.000
EAR	17.000	28.000	21.000	25.000	28.500	16.000	44.200	25.000	21.100	16.000
HF	13.800	14.200	8.800	8.600	12.700	16.800	21.200	10.000	12.200	12.300
TIBIA	49.200	20.400	13.500	13.400	17.400	12.800	12.600	16.700	16.900	45.400
FOREARM	50.000	64.400	45.600	48.400	58.600	44.700	45.400	58.700	58.100	45.400
3M META	19.400	64.500	46.300	50.000	59.200	44.700	46.700	59.000	56.100	45.400
3M 1PHAL	17.400	25.300	19.600	21.300	22.400	16.400	18.000	23.600	23.000	19.300
3M 2PHAL	16.200	24.800	17.600	18.400	22.200	16.700	18.000	21.600	55.100	15.300
4 META	47.800	62.100	44.600	48.600	56.500	13.800	45.200	55.700	17.900	44.800
4M 1PHAL	16.200	21.200	16.600	18.200	15.800	8.200	17.200	19.600	15.100	16.800
4M 2PHAL	8.100	8.400	10.300	2.600	16.000	26.900	2.400	37.700	33.400	2.700
5M META	30.000	38.100	27.900	28.600	34.500	13.200	26.000	32.400	16.200	26.400
5M 1PHAL	14.200	17.900	13.300	14.400	16.000	5.600	7.000	16.100	12.000	13.700
5M 2PTIP	6.600	11.700	6.200	7.200	9.800	6.600	7.600	10.000	4.100	5.900
3M TIP	3.500	4.600	3.100	2.800	11.000	2.300	2.800	7.600	21.400	18.100
UP CANIN	19.400	24.300	18.800	20.600	23.700	16.000	19.000	22.200	21.400	17.100
GSL	7.400	24.400	17.800	19.400	23.500	16.100	18.200	22.500	0.000	5.400
CON INCI	5.800	9.600	7.600	9.000	9.500	5.100	5.200	8.500	15.700	4.200
ROST LEN	13.300	7.500	6.600	6.400	6.400	4.600	12.800	6.300	9.700	12.000
LACR WID	8.200	17.000	12.400	13.300	16.700	10.700	17.800	9.300	2.000	7.100
INTORB W	1.400	10.400	7.400	8.300	9.600	6.600	1.200	1.500	4.500	1.200
CON CANI	3.400	2.000	1.200	1.600	1.600	1.100	1.100	1.800		1.300
LOWER TR	5.000	4.800	3.700	4.100	5.100	3.800	3.800	4.700	14.300	3.400
TR CCN H	12.600	4.500	3.800	3.500	5.800	2.600	3.600	3.700	11.600	3.600
DENTHIC	10.400	15.500	11.400	12.200	15.800	9.800	10.600	13.800	12.400	10.600
MOM1 COR	11.600	12.300	9.700	9.800	12.800	8.100	9.000	11.200	8.800	8.600
MOM2 ANG	8.000	14.300	10.700	11.600	13.600	6.800	10.000	13.000	8.200	10.000
POST ORB	6.400	10.000	7.700	8.600	9.000	6.800	6.100	9.400	8.100	6.400
ZYGO BR	7.400	8.600	7.000	7.600	8.700	5.900	6.900	7.900	2.300	6.800
8CASE BR	2.000	9.300	7.000	1.200	8.700	5.000	6.000	8.300	2.300	6.800
MASTOIDB	2.600	1.100	1.800	2.200	2.200	1.800	2.000	2.000	2.300	1.700
PALATE L		2.600	2.400	2.400	3.100	2.300	2.000	2.500	2.600	2.000

	T AEGYPA	T AFRICA	T ANSORA	T AURISA	T AUSTRA	T BRASIA	T FEMORA	T FULMIN	T KUBCRI	T LATICA
M3 M3	4.900	6.200	5.000	0.800	5.800	3.700	4.200	5.400	0.0	4.200
ANT PTER	3.900	2.400	2.700	2.000	3.100	2.230	1.900	2.300	2.830	1.900
POSTPTER	3.000	3.600	2.900	3.000	4.300	2.400	2.800	3.200	3.430	2.800
LO CANIN	3.300	4.600		2.900	3.800	2.000	2.800	3.800	0.0	2.400
DENT LEN	14.000	17.500	12.900	14.400	17.200	11.400	13.200	16.000	15.900	12.400
FOR ANT	12.100	14.900	11.900	12.500	14.400	9.800	11.200	13.400	13.430	10.800
ANGUL L	2.700	3.600	2.800	2.900	3.400	2.200	2.600	4.700	4.600	2.600
CDN CORO	4.000	5.100	3.400		5.000	3.000	3.900		11.500	3.500
COND M1	10.200	12.600	9.400	10.400	12.800	8.400	9.800	11.700	2.800	9.000
ANGUL M	2.300	3.200	2.200	2.800	2.600	1.800	2.400	2.300	4.600	2.800
CORO HT	4.000	4.800	3.200	3.600	4.000	3.100	2.800	4.000	1.003	3.200
INCI FOR	2.000	3.000	3.000	1.000	2.000	1.000	1.000	3.000	1.003	1.000
N SHAPE	3.000	4.000	3.000	4.000	2.000	2.000	2.000	4.000	1.000	3.000
PREMOLAR	3.000	1.000	2.000	3.000	1.000	1.000	1.000	1.000	2.000	2.000
BASI PIT	1.000	2.000	1.000	2.000	2.000	1.000	1.000	2.000	2.030	2.000
A SAGITT	1.000	2.000	3.000	2.000	3.000	3.000	2.000	2.000	3.020	3.000
P SAGITT	1.000	3.000	1.000	3.000	2.400	1.600	3.000	2.600	2.300	3.000
EAR JUNC	3.000	2.000	1.800	2.200	2.800	1.200	1.700		1.800	1.400
WRINKLES	1.800	3.000	1.400	1.400	6.600	4.500	1.400	2.400	6.203	4.800
MI META	1.400	6.700	5.100	5.800	3.000	2.000	5.500	2.600	3.000	2.000
GLENO L	5.500	3.000	2.000	1.000	2.000	2.000	2.000	6.000	1.000	
GLENO W	2.000			2.000				2.000		
UP MOL R	2.000		92.900	96.900	114.800	83.700	91.300	111.800	114.200	86.000
HAIRYNES	94.400	124.000	70.900	69.400	89.900	64.700	64.800	83.000	88.100	63.700
L LAMBDO	72.100	91.700	47.400	50.000	60.900	45.700	46.100	58.500	58.030	46.100
S LAMBDO	50.800	67.700	2.905	2.926	2.847	2.790	2.965	2.915	2.971	2.855
DIGIT 3	2.827	2.783	66.880	66.690	66.210	65.650	66.790	65.570	66.287	65.350
DIGIT 4	65.700	65.700	1.943	1.938		1.832	1.980	1.911	1.969	1.866
DIGIT 5	1.858	1.832	0.461	0.517	0.486	0.365	0.467	0.426	0.361	0.351
ASPECT	0.346	0.435	0.109		0.070	0.096	0.091	0.094	0.088	0.097
TIP INDX	0.114	0.114	0.093	0.111	0.093	0.088	0.083	0.112	0.126	0.105
D3 I D5	0.100		0.581	0.528	0.512	0.509	0.515	0.525	0.541	0.556
EAR 1 FA	0.514	0.554	0.248	0.250	0.244	0.272	0.212	0.262	0.302	0.258
CONHT DL	0.286	0.274								
DTHIC DL										
MI+M2 DL										
COR H DL										

135

The table below transposes the page's rotated layout: measurement variables are listed as rows (left column) and taxa as columns.

Variable	T LOBATA	T MACROA	T TENIDA	TC ALOYA	TC BIVIA	TC CHAPI	TC BEMMI	TC JOBEN	TC JOHOR	TC MAJOR
HEAD BOD	78.000	86.000	86.000	80.500	81.000	56.000	0.0	85.000	60.000	65.000
TAIL	52.500	49.500	44.000	41.500	38.500	28.000	0.0	41.000	32.000	26.000
EAR	30.500	33.000	30.800	22.000	21.600	14.000	0.0	23.000	20.000	18.100
HF	9.800	10.200	10.800	9.800	11.800	7.500	0.100	10.000	14.300	17.100
TIBIA	18.200	16.000	16.600	15.600	14.500	10.600	9.100	14.300	9.300	42.200
FOREARM	61.000	60.000	60.400	52.400	49.200	33.900	0.0	48.300	46.400	41.900
3M 1PHAL	23.900	23.400	62.000	53.000	50.100	13.000	46.400	48.300	46.100	16.800
3M 2PHAL	22.600	21.100	23.200	21.400	21.400	13.500	47.000	19.600	18.600	16.600
4 META	50.100	58.400	21.200	20.700	48.400	31.500	19.800	19.600	17.200	41.100
4 M 1PHAL	20.500	19.500	58.400	51.200	16.800	9.900	17.800	45.900	45.400	14.100
4 M 2PHAL	12.800	12.800	19.300	16.400	11.400	9.900	45.300	15.500	14.700	10.900
5 META	37.200	30.900	10.300	11.600	30.000	21.400	15.900	12.200	11.200	25.900
5M 1PHAL	16.400	16.400	35.400	31.600	16.600	5.400	11.300	28.500	28.900	12.600
5M 2PTIP	11.300	8.000	17.100	14.300	6.600	4.400	28.800	14.900	11.600	8.600
3M TIP	4.100	3.000	10.800	9.100	3.500	2.300	13.400	16.300	10.200	2.900
UP CANIN			10.300	3.400	3.500		9.200	6.400		
GSL	23.000	23.000	24.000	21.200	18.900	15.900	9.200	21.200	17.200	17.300
CON INCI	23.000	21.600	23.400	19.600	18.600	6.100	2.700	19.600	17.300	16.900
ROST LEN	9.400	9.700	10.000	8.600	7.900	1.400	12.900	8.300	8.300	7.300
LACR WID	5.800	6.600	6.000	7.200	7.400	9.600	16.900	8.200	6.600	6.900
INTORB W	15.700	4.500	6.000	5.200	5.300	5.900	6.700	5.200	5.300	5.030
CON CANI	9.600	15.700	9.400	13.000	13.000	1.500	6.100	13.700	12.400	7.300
LOWER TR	1.800	9.400	1.200	8.100	8.100	2.900	4.400	8.700	7.500	1.400
TR CON H	3.800	1.300	1.400	1.400	1.700	3.600	11.600	1.800	2.300	3.500
DENTHIC	5.000	1.800	4.700	4.400	4.900	7.900	1.900	2.000	3.800	3.200
MOM1 COR	14.700	3.400	3.700	3.800	3.900	6.000	1.400	4.200	3.300	11.500
MOM2 ANG	13.100	4.700	4.800	4.600	4.900	5.700	3.500	4.800	3.300	11.800
POST ORB	10.100	12.700	14.800	12.400	12.400	5.400	3.300	13.300	11.700	7.300
ZYGO BR	7.200	10.700	13.100	10.400	10.400	0.900	11.000	10.600	10.700	6.600
BCASE BR	8.400	9.800	9.700	8.400	8.000	6.000	10.800	11.700	7.500	1.700
MASTOIDB	1.400	8.800	7.400	7.600	7.600	5.700	6.300	8.300	6.800	2.300
PALATE L	1.200	1.400	8.800	7.500	7.000	5.400	6.300	7.400	6.800	
BCASE HT	2.400	2.100	1.400	1.100	1.100	0.900	1.000	1.100	1.200	
M3 LENG		2.500	2.200	1.800	2.100	2.100	1.800	2.200	1.700	
M3 WIDTH			3.200	2.600	2.400		2.400	2.700	2.100	
C1 C1										

	T LOBATA	T MACROA	T TENIOA	TC ALOYA	TC BIVIA	TC CHAPI	TC BEMMI	TC JOBEN	TC JOHOR	TC MAJOR
M3 M3	5.200	5.500	5.600	5.400	5.400	4.900	4.600	5.900	4.700	4.900
ANT PTER	2.200	2.800	3.600	2.400	2.400	1.900	2.700	2.300	2.600	2.900
POSTPTER	3.600	2.900	3.400	3.000	3.200	0.0	2.400	3.100	3.400	2.800
LO CANIN	3.200	2.900	3.000	3.000	3.100	1.900	2.460	3.100	2.400	3.000
DENT LEN	16.000	15.900	17.700	14.300	13.900	10.000	12.300	14.300	12.300	12.300
FOR ANT	14.000	13.800	14.700	12.000	11.600	8.400	11.600	12.300	10.800	10.500
ANGUL L	4.800	4.500	4.800	4.400	4.100	1.800	3.600	4.300	2.700	2.600
CON CORO	11.500	11.600	12.300	10.400	9.800	2.900	9.800	10.300	9.500	9.100
COND M1	2.500	2.400	2.300	2.800	3.500	7.700	2.800	3.600	2.330	2.400
ANGUL M	4.200	3.000	4.100	3.500	3.500	2.600	3.100	4.300	3.500	3.300
CORO HT	4.000	3.000	4.000	3.000	3.000	2.000	2.000	2.000	2.000	3.000
INCI FOR	3.000	1.000	1.000	4.000	3.000	3.000	3.000	2.000	3.000	2.000
N SHAPE	4.000	4.000	3.000	1.000	1.000	1.000	3.000	3.000	1.000	1.000
PREMOLAR	3.000	3.000	1.000	3.000	3.000	1.000	3.000	3.000	1.000	2.000
BAS1 PIT	1.000	1.000	1.000	1.000	1.000	3.000	1.000	3.000	3.000	3.000
A SAGITT	4.000	4.000	3.000	3.000	2.000	2.000	2.000	2.000	1.000	2.000
P SAGITT	2.000	2.000	2.000	2.000	2.200	2.500	1.900	2.500	1.900	1.800
EAR JUNC	3.000	3.000	2.900	2.200	1.600	1.600	2.000	1.700	1.000	2.400
WRINKLES	2.300	1.600	2.400	1.600	5.200	1.700	1.300	1.700	2.100	5.200
M1 META	2.400	6.400	2.500	6.200	3.000	4.300	1.800	5.500	5.400	2.000
GLENO L	1.600	1.000	6.600	2.000	3.000	3.000	4.000	5.500	3.000	
GLENO W	6.200	2.000	2.000	3.000	2.000	2.000	1.000	1.000	1.000	
CONDY L	2.000			2.000		1.000	2.000	3.000		
UP MOL R	2.000	1.000	2.000	2.000	2.000		2.000			
HAIRYNES										
L LAMBDO	2.000									
S LAMBDO	1.000									
DIGIT 3	116.800	111.100	117.500	104.200	99.500	66.100	93.800	96.800	93.100	83.900
DIGIT 4	89.100	80.700	88.300	79.300	76.700	50.800	72.500	73.600	71.300	66.900
DIGIT 5	64.600	58.300	62.300	53.300	50.700	35.900	49.000	48.600	46.000	43.800
ASPECT	2.721	2.935	2.856	2.938	2.933	2.857	2.850	2.973	3.033	2.879
TIP INDX	66.440	64.540	66.050	66.540	66.963	66.100	66.907	66.710	66.740	66.500
D3 I D5	1.808	1.906	1.886	1.955	1.963	1.889	1.907	1.984	2.024	1.916
EAR I FA	0.517	0.550	0.510	0.420	0.427	0.413	0.476	0.476	0.431	0.427
CONHT DL	0.099	0.071	0.082	0.099	0.125	0.150	0.157	0.126	0.155	0.130
DTMIC DL	0.111	0.082	0.082	0.099	0.110	0.100	0.116	0.140	0.101	0.114
M1+M2 DL	0.519	0.491	0.500	0.577	0.581	0.550	0.562	0.629	0.550	0.545
COR H DL	0.259	0.201	0.241	0.246	0.257	0.260	0.256	0.301	0.271	0.268

	TC NIGEA	TC PLICA	TC PUMIA	TC RUSSA	TM BRACH	TM CONDA	TM CONGA	TM DEMOA	TM LEONA	TM MIDAA
HEAD BOD	70.500	67.000	64.500	66.700	0.0	84.000	89.500	72.000	63.000	101.500
TAIL	35.500	36.500	36.500	31.500	30.000	44.000	58.500	31.000	30.500	44.000
EAR	18.500	17.500	18.000	19.500	15.000	17.000	24.000	16.000	18.500	27.500
HF	10.800	9.200	8.030	13.600	8.000	11.300	13.000	8.400	7.300	11.400
TIBIA	12.800	13.700	12.200	13.600	9.000	13.700	19.400	12.500	11.200	17.800
FOREARM	44.800	45.500	41.000	45.000	36.200	46.000	55.100	44.200	35.800	61.700
3 META	45.500	46.400	42.400	46.600	40.200	47.800	57.900	44.200	37.300	62.200
3M 1PHAL	18.900	17.600	17.500	20.000	16.500	21.100	25.600	17.300	13.400	24.400
3M 2PHAL	18.600	17.600	17.000	19.000	16.500	21.100	25.900	17.300	13.400	25.600
4 META	44.600	44.200	40.800	45.400	39.300	46.500	56.800	42.900	36.100	61.600
4M 1PHAL	15.600	14.300	14.300	15.400	13.200	17.600	21.600	13.600	11.500	20.600
4M 2PHAL	12.400	10.800	11.800	10.600	11.200	15.800	16.800	11.900	8.400	16.700
5 META	14.000	26.900	27.600	28.300	26.800	32.000	32.400	27.400	24.400	37.200
5M 1PHAL	6.000	16.000	15.000	13.000	10.300	13.200	15.800	12.600	9.600	17.400
5M 2PTIP	8.800	6.000	7.900	6.200	5.900	6.800	9.600	6.800	5.000	10.700
3M TIP	18.800	8.000	13.000	8.200	2.800	10.500	4.600	3.400	4.400	11.600
UP CANIN	8.400	3.400	4.000	2.800	2.800	4.800	25.200	20.000	17.600	5.600
GSL	8.700	19.200	17.400	18.800	18.400	20.700	24.400	19.200	16.500	27.400
CON INCI	5.000	17.600	16.200	17.200	17.300	18.600	9.800	8.200	7.200	25.600
ROST LEN	12.800	7.400	7.200	6.400	6.800	8.300	9.400	7.200	6.100	10.500
LACR WID	7.900	7.000	6.400	4.800	6.800	6.100	6.800	5.200	4.700	9.700
INTORB W	1.200	5.000	4.600	12.000	12.400	13.400	10.600	13.500	11.500	18.800
LOWER CAN1	3.800	12.400	11.200	1.100	2.400	4.700	2.200	1.900	6.800	11.000
LOWER TR	4.200	1.400	1.600	1.300	2.100	2.100	2.500	1.900	1.800	2.000
TR CCN H	11.800	1.400	3.300	3.600	1.700	1.800	5.200	1.200	1.500	2.600
DENTTHIC	9.600	3.800	3.200	3.600	3.800	4.300	5.800	4.200	3.800	5.700
MOM1 COR	11.000	3.800	4.000	4.300	3.800	4.300	5.000	4.400	4.000	6.000
MOM2 ANG	6.600	4.000	10.800	11.200	4.300	13.000	15.800	3.800	12.100	4.900
POST ORB	7.000	11.200	10.200	10.600	12.300	10.700	12.500	12.700	10.800	17.400
ZYGO BR	1.000	9.400	10.100	7.200	10.300	12.700	13.900	10.100	10.800	13.400
BCASE BR	2.000	10.300	6.400	6.500	11.500	7.200	9.900	11.400	7.400	14.700
MASTOIDB	2.400	6.800	6.200	1.800	17.900	7.200	9.100	6.800	6.600	11.500
PALATE L		7.200	1.700	2.400	6.300	2.000	1.100	7.400	6.200	8.800
BCASE HT		6.500	2.400		6.500	2.900	2.200	0.800	0.800	10.000
MITR		1.800			0.900		3.400	2.800	1.600	1.100
M3 LENG		2.600			1.700				2.600	2.500
M3 WIDTH					2.900					3.600
C1 C1										

138

	TC NIGEA	TC PLICA	TC PUMIA	TC RUSSA	TM BRACH	TM CONDA	TM CONGA	TM DEMDA	TM LECNA	TM MIDAA
M3 M3	4.900	5.100	4.600	5.000	5.300	6.000	7.000	5.600	5.200	7.800
ANT PTER	2.100	2.100	2.600	2.400	2.600	2.600	2.800	2.200	2.300	3.000
POSTPTER	2.600	2.800	2.400	2.800	2.400	2.800	3.400	2.800	2.600	3.500
LO CANIN	3.100	3.000	2.700	2.600	3.000	3.300	3.400	3.400	2.700	4.600
DENT LEN	13.200	12.800	11.000	12.600	12.800	13.800	17.500	14.000	11.000	19.300
FOR ANT	11.200	11.000	10.000	10.400	11.000	11.800	14.600	12.000	10.000	16.400
ANGUL L	2.800	2.800	2.400	2.800	3.000	3.500	4.300	4.400	3.800	6.000
CON CORO	3.800	3.900	3.400	3.700	4.200	4.400	5.400	4.400	3.800	4.600
COMO M1	9.800	9.000	8.000	9.100	9.700	10.400	13.400	10.000	8.000	14.800
ANGUL W	2.300	2.800	2.700	2.500	2.800	3.500	4.500	3.800	3.500	5.500
CORO HT	3.400	3.400	3.200	3.200	3.500	4.100	2.000	5.000	5.000	5.000
INCI FOR	2.000	2.000	2.000	2.000	2.000	2.000	5.000	4.000	3.030	2.000
N SHAPE	3.000	2.000	2.000	3.000	4.000	2.000	5.000	2.000	2.000	3.000
PREMOLAR	3.000	4.000	3.000	3.000	4.000	2.000	3.000	3.000	2.000	3.000
BASI PIT	3.000	3.000	1.000	1.000	3.000	3.000	2.000	3.000	3.030	2.000
A SAGIT1	1.000	2.000	3.000	1.000	1.000	3.000	3.000	2.000	2.000	2.000
P SAGIT1	3.000	3.000	3.000	3.000	3.000	3.000	2.700	2.300	1.930	3.500
EAR JUNC	2.000	2.000	1.800	2.000	2.000	2.200	2.030	2.400	1.600	2.700
WRINKLES	1.800	1.900	1.200	2.000	1.900	1.700	2.300			
M1 META	1.400	1.500	1.600	1.400	1.600					
GLENO L	5.200	5.100	4.600	4.900	5.000	5.600	6.800	5.600	4.800	7.600
GLENO W	3.000	3.000	3.000	3.000	3.000	3.000	3.000	3.000	3.000	3.000
CONDY L	2.000	2.000	2.000	2.000	1.000	3.000	1.000	1.000	1.000	1.000
HAIRYNES										
UP MOL R										
L LAMBDO										
S LAMBDO										
DIGIT 3	91.900	89.100	84.800	93.800	79.100	109.400	116.000	86.100	69.570	124.400
DIGIT 5	72.800	66.300	66.900	71.400	64.200	79.900	88.200	68.400	56.800	98.900
DIGIT 4	48.200	47.700	46.200	47.500	41.300	52.000	57.600	47.200	38.800	65.320
ASPECT	2.836	2.822	2.723	2.922	2.804	2.815	2.970	2.725	2.714	2.850
TIP INDX	67.230	66.200	67.410	67.580	68.310	68.580	67.600	66.950	66.050	66.905
D3 1 D5	1.907	1.868	1.835	1.975	1.915	1.931	2.014	1.824	1.791	1.905
EAR 1 FA	0.413	0.385	0.439	0.433	0.409	0.370	0.436	0.376	0.517	0.246
CONHT DL	0.144	0.109	0.138	0.089	0.164	0.152	0.137	0.136	0.151	0.104
DT MIC DL	0.091	0.109	0.112	0.105	0.133	0.130	0.143	0.129	0.126	0.135
M1+M2 DL	0.553	0.594	0.560	0.589	0.594	0.601	0.629	0.614	0.622	0.609
COR H DL	0.258	0.250	0.276	0.258	0.273	0.297	0.309	0.271	0.294	0.286

139

	TM MOPSA	TM NANUA	TM NIANG	TM NIVEI	TM SARAA	TM TREVO	TM THERA	XIPHONYC	TR ACETA	TR BECCA
HEAD BOD	66.500	57.000	91.000	79.000	71.000	89.000	72.500	59.000	47.000	62.000
TAIL	35.000	23.000	34.000	34.000	35.500	38.000	29.030	24.000	39.000	37.000
EAR	22.500	15.000	22.000	18.000	20.500	21.000	13.500	12.000	14.500	18.000
HF	10.000	7.000	13.200	9.500	10.500	17.600	8.000	7.300	6.520	8.300
TIBIA	14.800	9.000	52.100	13.700	14.400	55.600	12.600	12.600	10.400	12.500
FOREARM	43.700	30.000	53.000	46.300	41.200	54.300	37.200	28.400	38.600	34.700
3M META	18.600	11.200	22.900	47.200	42.500	24.300	38.800	29.100	39.400	36.600
3M 1PHAL	15.200	11.200	21.300	19.400	17.500	23.100	15.200	9.900	14.300	11.900
3M 2PHAL	41.400	29.000	51.300	18.900	14.400	53.400	37.300	10.300	12.300	34.700
4M META	10.700	9.600	18.000	45.400	40.200	11.600	12.600	27.900	12.400	10.600
4M 1PHAL	14.700	10.500	11.100	15.500	13.800	35.500	10.930	7.000	29.200	8.500
4M 2PHAL	11.800	10.700	31.600	12.700	9.600	7.900	25.600	19.400	6.600	25.000
5M META	27.000	20.000	7.600	29.100	24.800	9.500	4.800	6.600	5.700	4.700
5M 1PHAL	5.700	3.800	9.500	13.400	10.500	3.800	3.400	3.500	2.130	3.700
5M 2PTIP	3.100	3.600	23.000	6.400	7.400	23.300	18.800	3.700	14.600	18.400
3M TIP	21.200	4.600	21.800	8.400	2.900	21.800	17.500	0.000	14.100	18.500
UP CANIN	19.600	15.200	9.300	21.000	19.300	9.400	6.800	14.900	6.900	8.000
GSL	8.400	14.600	6.600	20.100	18.400	6.800	5.100	14.700	9.300	7.600
CON INC1	5.800	5.800	15.900	8.600	7.400	15.800	12.700	5.300	5.800	6.200
POST LEN	13.700	4.300	9.700	7.400	5.600	9.700	7.400	6.100	1.700	12.700
LACR WID	7.600	13.700	2.500	5.400	12.900	2.500	2.500	4.400	1.000	2.500
INTORB W	2.000	7.600	2.600	14.300	6.900	2.000	1.800	10.600	3.300	1.900
CON CANI	4.200	2.000	4.900	8.600	1.900	4.900	4.030	6.500	2.100	1.500
LOWER TR	4.800	1.600	5.900	2.200	1.800	5.100	3.930	1.500	8.300	3.800
TR CON H	13.100	3.000	14.700	1.900	4.400	14.500	12.000	1.000	7.300	4.0
DENTTHIC	11.000	3.600	13.600	4.400	4.500	13.900	9.600	3.100	6.100	9.400
MOM1 COR	12.200	13.800	9.300	4.100	10.300	9.300	11.200	3.400	6.600	8.100
MOM2 ANG	7.400	10.200	7.900	13.800	11.300	8.600	8.000	3.900	5.500	6.500
POST ORB		8.400		12.600	11.700			10.200	5.000	
ZYGO BR		9.400		12.500	6.700			7.900	6.400	
BCASE BR		5.800		7.700	6.700			9.600	6.100	
MASTOIDB	0.800	5.600	1.000	1.000	0.700	1.000	1.600	6.400	6.600	1.100
PALATE L	1.800	0.700	2.200	2.100	1.800	3.400	2.600	5.500	5.500	2.400
BCASE HT	2.800	1.400	3.100	3.100	2.600			5.900	5.000	
MTR		2.100						0.600	0.930	
M3 LENG								1.500	1.600	
M3 WIDTH								1.800	2.200	
C1 C1										

140

	TM MOPSA	TM NANUA	TM NIANG	TM NIVEI	TM SARAA	TM TREVO	TM THERA	XIPHONYC	TR ACETA	TR BECCA
M3 N3	6.000	4.800	6.500	6.100	6.000	6.400	5.000	4.300	3.030	4.300
ANT PTER	2.800	2.000	2.700	2.600	2.800	2.900	2.200	2.000	1.400	1.900
POSTPTER	3.000	2.400	2.800	2.900	2.800	3.300	2.600	2.000	1.700	2.400
LO CANIN	2.800	2.400	4.100	3.700	2.600	3.500	2.800	2.500	2.000	3.100
DENT LEN	14.100	10.800	16.300	14.800	13.400	16.300	13.000	10.600	10.400	13.100
FOR ANT	12.400	9.200	13.700	12.500	11.400	13.500	11.200	8.900	8.800	11.000
ANGUL L	3.200	2.400	3.900	3.700	3.400	4.000	3.000	2.500	2.200	2.800
CON CORO	4.400	3.200	5.000	5.000	3.400	5.200	4.030	3.000	3.000	4.000
COND M1	10.800	8.000	12.000	11.200	10.200	12.200	9.700	8.100	7.600	10.000
ANGUL W	3.200	2.800	4.700	3.900	3.400	4.500	2.600	2.600	1.000	2.700
CORO HT	2.700	2.700	2.000	2.600	3.900	2.000	3.800	3.400	3.200	5.500
INCI FOR	3.000	3.000	4.000	4.000	2.000	3.000	3.000	3.000	1.000	4.000
N SHAPE	6.000	5.000	3.000	2.000	6.000	3.000	4.000	5.000	4.000	4.000
PREMOLAR	1.000	3.000	2.000	2.000	1.000	3.000	3.000	4.000	1.000	2.000
BASI PIT	3.000	3.000	2.000	2.000	3.000	2.000	3.000	2.000	2.000	1.000
A SAGITT	2.000	1.000	1.000	2.000	2.000	2.000	2.000	2.000	2.000	1.000
P SAGITT	1.000	1.000	3.000	2.000	3.000	2.000	1.000	3.000	1.000	1.000
EAR JUNC	3.000	3.000	1.000	2.000	2.000	2.000	2.000	2.000	1.000	1.000
WRINKLES	2.000	2.000	2.700	2.000	2.000	2.800	3.000	3.000	3.000	3.000
M1 META	2.300	2.000	2.900	2.600	2.200	2.830	2.000	1.400	1.200	2.100
GLENO L	2.400	2.000	6.100	6.000	2.200	6.500	2.100	2.100	1.400	1.500
GLENO W	1.400	1.400	3.000	2.000	1.600	6.000	2.200	1.400	1.100	1.300
CONDY L	5.000	4.000	3.000	6.000	5.600	6.500	1.600	4.100	1.400	2.000
UP MOL R	3.000	3.000	3.000	3.000	3.000	6.500	5.000	1.000	2.000	2.000
HAIRYNES	1.000	3.000	3.000	3.000	1.000	1.000	1.000	3.000	1.400	1.300
S LAMBDO	3.000	3.000	3.000	3.000	3.000	3.000	1.000	3.000	2.000	2.000
DIGIT 3	84.200	57.200	106.900	94.000	81.500	112.100	76.800	53.100	72.300	68.200
DIGIT 4	66.600	46.400	80.400	73.600	63.600	84.800	60.600	43.100	60.200	53.800
DIGIT 5	44.500	31.200	53.300	48.900	40.700	55.600	40.200	29.500	44.400	37.200
ASPECT	2.874	2.763	2.983	2.869	3.015	2.980	2.843	2.759	2.475	2.766
TIP INDX	65.800	66.360	67.230	67.000	66.420	67.650	67.280	65.116	65.190	66.280
D3 I D5	1.892	1.833	2.006	1.922	2.002	2.016	1.913	1.797	1.614	1.833
EAR I FA	0.515	0.517	0.422	0.389	0.485	0.392	0.363	0.423	0.376	0.519
CONHT DL	0.142	0.148	0.153	0.149	0.142	0.153	0.192	0.142	0.163	0.191
DTH1C DL	0.128	0.111	0.147	0.128	0.134	0.123	0.138	0.128	0.096	0.145
M1+M2 DL	0.610	0.556	0.632	0.622	0.627	0.607	0.608	0.585	0.557	0.634
COR H DL	0.284	0.250	0.288	0.284	0.291	0.276	0.292	0.321	0.308	0.420

	TR JUGUA	TR KALIN	TR LORIA	TR MINUA	TR NORFA	TR PHRUD	TR PLANA	C PARVID	C TORGUA	CP BRACA
HEAD BOD	65.500	51.000	51.000	47.500	55.500	57.000	56.200	133.000	132.000	82.500
TAIL	14.000	27.000	27.000	21.700	32.500	30.000	24.600	47.000	47.000	38.500
EAR	9.700	13.000	13.000	12.300	12.000	11.000	14.400	28.200	27.700	9.600
HF	10.200	5.800	5.400	6.300	6.600	7.400	6.700	22.200	21.000	11.600
TIBIA	39.000	36.500	30.100	7.700	9.400	9.300	9.300	30.900	31.600	43.600
FOREARM	37.400	12.800	33.100	29.000	32.800	35.300	35.000	75.700	75.400	48.000
3 META	14.400	12.600	12.600	30.700	34.500	37.200	35.000	80.100	79.100	21.200
3M 1PHAL	13.100	13.100	12.800	11.100	12.700	12.800	13.200	45.200	44.100	18.100
3M 2PHAL	35.900	36.000	32.800	10.900	12.700	11.500	12.600	78.300	76.700	45.700
4 META	12.800	11.100	11.000	29.900	33.600	36.000	34.100	37.100	36.100	18.500
4M 1PHAL	9.100	7.100	7.200	10.000	10.600	10.800	10.000	23.300	23.300	20.600
4M 2PHAL	24.600	23.600	23.800	6.600	10.200	4.900	10.000	42.000	29.700	12.800
5 META	8.900	5.200	8.000	20.800	24.900	24.300	25.000	29.800	9.700	6.000
5M 1PHAL	5.200	5.600	4.600	8.600	7.400	9.300	8.100	9.400	9.600	5.200
5M 2PTIP	6.000	2.300	2.300	3.400	6.200	4.300	6.400	15.000	14.500	4.000
3M TIP	2.400	15.500	14.800	2.300	2.200	2.300	2.400	14.700	14.500	
UP CANIN	16.700	15.500	14.400	13.400	15.000	15.200	15.200	30.600	29.300	20.400
GSL	16.500	14.500	14.400	13.400	14.900	15.500	15.200	27.800	28.300	20.600
CON INC1	7.300	6.000	6.400	6.500	6.100	6.200	6.500	12.300	12.600	8.200
ROST LEN	5.600	6.400	5.800	4.400	5.000	6.200	4.800	13.100	10.200	9.200
LACR WID	11.200	4.400	9.900	9.000	5.000	10.500	10.000	11.100	21.400	8.100
INTORB W	6.400	10.000	5.800	4.400	6.000	6.200	6.000	21.400	12.000	14.700
CON CAN1	2.100	5.900	5.600	5.200	6.000	6.200	6.000	12.000	3.200	8.700
LOWER TR	1.500	1.000	1.200	1.400	1.200	1.300	2.200	3.500	7.500	2.100
TR CON H	3.800	1.500	3.200	1.100	3.400	1.800	1.100	7.500	8.000	4.000
DENTTH1C	3.300	3.800	2.600	2.800	2.800	2.700	3.500	8.100	7.900	5.200
MOM1 COR	3.700	2.700	3.700	2.400	3.800	3.100	2.500	7.800	20.500	10.800
MOM2 ANG	10.000	3.300	3.700	3.400	3.800	3.900	3.800	21.000	13.700	14.400
POST ORB	10.000	9.300	8.700	7.000	8.400	0.0	3.900	14.500	19.700	9.000
ZYGO BR	7.200	8.500	7.600	7.000	6.600	7.000	7.700	19.900	13.300	7.800
BCASE BR	5.400	6.600	6.400	5.900	6.600	4.800	6.500	13.600	10.400	1.000
MASTOIDB	6.000	5.200	5.400	4.600	5.000	5.700	4.500	9.600		2.800
PALATE L	1.000	5.800	5.400	0.800	5.400	1.800	5.400	10.600	10.400	
BCASE HT	1.900	1.100	1.000	1.500	1.000	2.200	1.000	1.400	1.300	
MTR	2.500	1.700	1.700	1.800	1.800		1.800	2.800	2.700	
M3 LENG		2.300	2.100		2.400		2.400	4.600	4.600	
M3 WIDTH										
C1 C1										

Data matrix (rows = craniodental variables; columns = taxa/samples). Values as read from the rotated table.

	TR JUGUA	TR KALIN	TR LORIA	TR MINUA	TR NORFA	TR PHRUD	TR PLANA	C PARVID	C TORCUA	CP BRACA
M3 M3	1.700	3.500	3.400	3.200	3.800	3.700	3.600	8.700	8.000	5.900
ANT PTER	2.600	1.900	1.300	1.800	2.000	1.900	1.400	3.700	4.300	2.100
POSTPTER	2.300	1.900	1.900	1.900	2.000	2.100	2.100	4.100	4.200	3.200
LO CANIN	2.000	0.000	2.100	1.400	2.000	2.000	2.200	4.600	4.300	3.500
DENT LEN	11.700	10.700	10.400	9.400	10.600	9.000	10.700	22.600	22.000	15.500
FOR ANT	2.900	8.800	8.900	8.100	9.200	9.000	9.300	19.400	18.300	12.400
ANGUL L	2.900	2.300	2.200	1.800	2.300	2.400	2.100	5.900	5.800	3.800
CON CORO	3.700	3.100	2.200	2.800	3.200	3.100	3.100	17.400	16.900	11.400
COND M1	8.800	7.700	7.800	7.100	8.000	8.100	8.100	4.000	3.600	2.800
ANGUL W	4.800	3.600	3.600	1.600	2.000	2.200	2.000	9.000	9.400	5.000
CORO HT	4.000	3.000	3.000	2.800	3.600	3.400	3.400	1.000	1.000	1.000
INCI FOR	4.000	4.000	4.000	3.000	4.000	3.000	4.000	1.000	1.000	1.000
N SHAPE	1.000	1.000	2.000	1.000	1.000	1.000	3.000	1.000	1.000	1.000
PREMOLAR	1.000	1.000	2.000	1.200	2.000	1.000	1.000	1.000	1.000	1.000
BASI PIT	1.000	1.000	1.000	1.000	2.000	1.000	1.000	1.000	1.000	2.000
A SAGITT	1.000	1.000	1.000	1.000	1.000	1.000	1.000	3.000	3.000	1.000
P SAGITT	2.000	2.000	2.000	1.000	1.000	1.000	3.000	1.000	1.000	1.000
EAR JUNC	3.000	3.000	1.000	2.000	3.000	3.000	1.000	1.000	1.000	1.000
WRINKLES	1.000	1.000	1.000	1.000	1.400	1.700	1.400	2.900	3.700	2.400
M1 META	1.500	1.400	1.400	1.300	1.600	1.500	1.600	2.300	2.600	1.800
GLENO L	1.900	1.100	1.000	0.900	1.200	1.200	4.400	8.700	8.800	6.100
GLENO W	4.700	4.300	1.000	3.800	4.200	4.500	2.000	2.000	2.000	3.000
CONDY L	2.000	2.000	2.000	2.000	2.000	2.000	2.000	2.000	2.000	2.000
UP MOL R	3.000	2.000	2.000	2.000	2.000	1.000	1.000	2.000	2.000	2.000
HA1RYNES	70.900	61.000	65.000	51.000	2.000	65.800	67.000	178.600	175.500	92.500
L LAMBDO	57.800	66.500	53.800	55.400	54.100	51.800	54.900	138.300	136.100	69.400
S LAMBDO	38.700	54.300	36.400	46.500	37.100	38.500	37.700	81.200	79.800	47.400
DIGIT 3	2.840	38.000	2.613	33.400	2.666	2.631	2.653	3.132	3.144	2.871
DIGIT 4	64.510	2.711	68.350	2.527	66.840	64.960	67.000	70.230	69.550	67.960
DIGIT 5	1.832	64.460	1.786	65.640	1.782	1.709	0.777	2.376	2.199	1.951
ASPECT	0.359	1.356	0.706	1.659	0.369	0.310	0.436	0.199	0.367	0.335
TIP INDX	0.179	0.140	0.154	0.149	0.132	0.164	0.131	0.177	0.191	0.139
D3 1 DS	0.128	0.093	0.115	0.117	0.113	0.118	0.103	0.155	0.164	0.132
EAR 1 FA	0.607	0.533	0.558	0.553	0.585	0.527	0.551	0.690	0.682	0.576
CONHT DL	0.359	0.308	0.346	0.298	0.340	0.309	0.336	0.398	0.427	0.331
DTP1C DL										
M1+M2 DL										
COR H DL										

143

	CP GREEA	CP PLANA	E AURIPA	E BONARA	E GLAUCA	E HANAMA	E MAURUS	E PEROTA	E UNDERA	MP TEMMA
HEAD BOD	61.000	51.000	91.000	74.500	99.500	75.000	63.000	109.000	110.500	48.500
TAIL	25.000	29.000	40.000	37.000	50.500	29.000	50.500	61.500	59.000	27.500
EAR	10.000	10.000	18.000	21.000	11.800	22.500	22.500	44.000	26.600	11.200
HF	7.200	5.700	12.200	8.400	12.600	10.200	9.500	13.400	14.600	5.800
TIBIA	9.400	8.100	14.400	11.800	19.000	8.600	16.700	21.500	21.300	31.200
FOREARM	35.200	31.700	58.000	46.900	60.600	38.800	53.100	74.700	68.300	33.100
3M META	37.200	34.400	61.200	50.200	62.300	39.600	54.300	77.700	73.300	12.900
3M 1PHAL	13.600	14.400	26.100	20.000	25.800	15.000	23.300	31.900	32.100	10.900
3M 2PHAL	13.400	12.800	24.000	17.600	24.200	14.700	21.600	29.100	29.700	32.000
4M META	35.400	32.800	58.000	49.000	60.200	38.000	51.700	75.000	71.200	10.800
4M 1PHAL	13.400	14.200	22.300	17.600	21.600	13.000	20.400	26.400	27.600	26.200
4M 2PHAL	3.600	4.200	6.000	7.200	5.000	3.000	6.100	6.400	40.600	5.200
5M META	22.400	21.700	32.400	29.200	34.300	21.100	30.100	41.800	22.600	5.000
5M 1PHAL	4.800	4.000	17.200	16.200	18.700	11.300	16.200	22.800	10.600	2.400
5M 2PTIP	9.500	3.600	9.000	7.200	7.600	2.830	6.400	12.900	9.600	13.200
3M TIP	3.600	2.800	8.800	3.400	6.200	2.800	3.800	5.700	5.800	5.400
UP CANIN	3.200	15.400	4.700	19.600	23.400	19.500	20.600	30.400	27.300	6.800
GSL	17.400	17.000	23.800	7.800	23.800	19.200	27.900	13.000	11.000	5.400
CON INCI	17.000	6.000	23.500	5.000	9.000	8.200	6.300	5.600	9.400	5.500
ROST LEN	12.100	6.700	9.200	13.600	8.100	4.700	4.600	22.400	20.400	2.000
LACR WID	1.800	10.800	8.000	8.600	6.100	12.900	18.900	13.100	12.600	1.200
INTORB W	1.400	6.500	6.400	1.700	16.800	1.800	1.300	1.800	2.600	3.200
CON CANI	3.100	1.700	16.800	3.800	10.400	1.800	4.300	2.100	5.900	3.800
LOWER TR	3.400	1.400	10.100	4.200	1.500	3.800	4.400	7.100	6.500	7.000
TR CON H	4.400	2.800	2.300	12.200	4.900	3.700	12.600	5.400	17.800	6.100
DENTHIC	11.800	3.400	2.900	11.400	4.900	4.200	9.700	17.800	13.300	4.600
MOM1 COR	8.200	4.200	5.600	8.100	14.600	11.600	10.600	13.300	15.400	5.400
MOM2 ANG	7.400	10.400	14.600	7.300	12.600	8.700	8.700	15.100	11.400	10.800
POST ORB	6.600	8.000	11.400	1.200	13.900	10.400	7.400	9.300	10.200	1.500
ZYGO BR	6.100	9.800	12.500	2.200	8.600	6.400	0.700	11.600	1.530	1.800
BCASE BR	0.800	5.600	10.400	2.100	6.600	7.200	1.900	2.700	2.600	
MASTOIDB	1.700	5.800	7.900		1.000	1.200				
PALATE L	2.200	1.600	9.200		2.400	2.330				
BCASE HT		2.100	1.100							
MTR			2.400							
M3 LENG										
M3 WIDTH										
C1 C1										

	CP GREEA	CP PLANA	E AURIPA	E BONARA	E GLAUCA	E HANAMA	E MAURUS	E PEROTA	E UNDERA	MP TEMMA
M3 M3	4.800	4.400	6.400	4.900	5.900	4.500	5.400	7.100	7.400	3.600
ANT PTER	1.600	1.500	2.400	2.100	2.300	2.600	1.900	3.400	3.000	1.400
POSTPTER	2.800	2.600	3.100	2.800	3.100	2.800	3.000	3.400	3.000	1.800
LO CANIN	2.900	2.600	4.600	3.000	4.200	3.000	3.700	5.200	5.000	2.000
DENT LEN	12.500	11.200	14.300	11.800	17.300	13.400	14.800	22.400	21.400	8.100
FOR ANT	10.500	9.200	14.900	11.200	14.800	11.700	12.600	19.400	18.000	2.400
ANGUL L	2.700	2.700	5.400	4.000	5.200	3.200	4.700	8.000	6.600	7.600
CON CORO	4.700	3.500	12.700	10.400	12.600	10.600	11.700	16.900	15.200	3.000
COND M1	9.200	8.600	5.300	2.600	3.800	2.600	2.700	5.200	4.600	4.000
ANGUL W	2.200	2.200	5.000	3.800	4.700	3.800	4.100	3.600	6.000	1.000
CORD HT	3.900	3.400	4.000	3.000	1.000	1.000	1.000	3.000	1.000	2.000
INCI FOR	1.000	1.000	3.000	4.000	4.000	3.000	1.000	1.000	4.000	1.000
N SHAPE	1.000	5.000	4.000	1.000	2.000	1.000	1.000	1.000	3.030	1.300
PREMOLAR	5.000	1.000	2.000	4.000	2.000	2.000	3.000	4.000	2.000	1.400
BAS1 PIT	1.000	1.000	2.700	2.000	2.000	4.000	1.000	2.000	2.000	1.100
A SAGITT	1.000	1.000	3.000	1.930	2.060	3.000	2.000	3.600	4.000	3.000
P SAGITT	1.000	1.000	2.000	1.190	2.700	1.800	4.000	3.200	3.200	2.000
EAR JUNC	1.000	1.500	1.000	2.200	6.700	1.900	2.000	2.300	2.700	
WRINKLES	1.800	1.100	1.500	5.600	2.000	5.400	2.300	8.500	8.130	
M1 META	1.400	4.800	4.800	2.000	3.000	2.000	2.500	3.000	3.000	
GLENO L	5.200	3.000	2.000	2.000	2.000	2.000	1.700	2.000		
GLENO W	3.000	1.000	1.000				6.100			
CONDY L	2.000						2.000			
UP MOL R							3.000			
HAIRYNES										
L LAMBDO										
S LAMBDO										
DIGIT 3	69.600	64.000	120.100	94.800	119.900	72.400	125.603	147.900	144.400	63.400
DIGIT 4	52.400	49.200	86.700	71.300	87.500	54.200	76.200	108.200	106.400	52.200
DIGIT 5	36.700	34.100	58.600	52.400	61.500	37.600	54.200	79.200	74.600	37.800
ASPECT	2.856	2.830	3.039	2.704	2.935	3.005	2.928	2.882	2.874	2.503
TIP INDX	66.400	67.150	67.430	66.430	66.430	65.110	66.540	68.417	67.790	67.020
D3 I D5	1.896	1.900	2.049	1.809	1.950	1.957	1.948	1.916	1.951	1.677
EAR I FA	0.355	0.315	0.314	0.448	0.195	0.580	0.358	0.590	0.381	0.353
CONHT DL	0.145	0.152	0.133	0.123	0.087	0.134	0.088	0.079	0.124	0.204
DTHIC DL	0.113	0.125	0.139	0.101	0.116	0.119	0.122	0.092	0.124	0.122
MI+P2 DL	0.548	0.554	0.607	0.551	0.595	0.560	0.581	0.548	0.590	0.551
COR H DL	0.315	0.304	0.306	0.275	0.272	0.284	0.277	0.228	0.286	0.306

	M ATERA	M BONDA	M COIBEA	M MOLOSS	M PRETIA	M SINALA	M TRINIA	M MYOP ALB	MYOP WHA	NEOPLATA
HEAD BOD	86.500	64.500	65.000	65.000	79.000	68.000	0.000	86.000	56.000	51.000
TAIL	43.500	35.500	31.500	35.000	38.500	42.000		41.000	27.000	24.000
EAR	16.500	12.800	12.800	12.000	13.000	12.000	8.200	22.000	13.000	13.300
HF	11.200	8.600	9.600	9.600	10.400	9.000	15.600	10.500	6.800	5.000
TIBIA	50.700	12.600	10.600	13.100	15.400	15.300	43.600	14.000	34.600	28.600
FOREARM	52.700	39.600	33.800	38.600	47.000	47.200	45.200	53.800	37.000	30.200
3 META	23.200	41.100	36.600	39.600	46.600	48.000	20.400	57.700	13.000	12.000
3M 1PHAL	51.000	19.000	16.100	18.100	21.100	21.000	17.400	20.400	35.800	29.600
3M 2PHAL	19.800	16.000	14.200	18.600	18.600	18.300	44.000	22.400	12.000	10.600
4 META	51.000	39.400	35.600	38.600	45.600	46.300	17.300	54.200	10.000	23.400
4M 1PHAL	19.800	16.100	14.600	15.700	18.100	17.800	28.800	16.800	25.400	36.100
4M 1PHAL	32.800	2.800	2.400	15.700	18.100	17.800	11.400	14.700		2.900
5 META	12.400	26.100	22.600	25.600	27.600	30.400	3.500	35.900	6.000	13.200
5M 1PHAL	7.600	10.900	9.900	10.200	11.500	12.000	18.400	15.800	2.900	15.700
5M 2PTIP	3.900	5.800	4.200	5.700	6.800	6.800	17.000	8.600	17.300	9.600
3M TIP	21.500	3.800	2.800	3.300	6.800	6.800	6.000	8.200	16.700	5.700
UP CANIN	20.500	3.500	15.900	17.200	3.500	3.500	5.000	4.200	7.000	1.200
GSL	8.200	17.800	14.900	16.500	20.300	18.200	12.600	23.500	4.600	2.600
CON INCI	7.200	16.400	5.300	6.500	19.400	18.200	7.600	23.000	11.500	39.300
ROST LEN	5.900	6.000	5.100	5.930	7.200	6.600	1.900	9.400	6.500	7.000
LACR WID	15.400	5.200	4.700	4.800	5.200	6.600	3.700	9.200	1.200	9.300
INTORB W	9.200	12.300	10.400	12.000	8.200	5.000	3.700	7.200	3.800	6.800
CON CANI	2.200	17.000	6.400	7.000	14.200	13.000	11.400	16.600	2.900	6.800
LOWER TR	4.900	1.800	1.600	1.300	8.200	7.800	11.000	9.600	4.000	5.400
TR CON H	5.400	3.800	3.400	3.800	1.800	1.500	6.700	2.200	8.390	1.900
DENTHIC	14.300	4.000	3.600	3.800	2.400	2.000	7.000	6.000	9.600	1.800
MOM1 COR	14.000	4.100	10.800	3.700	4.200	4.400	0.800	5.500	5.600	
MOM2 ANG	7.900	11.400	8.500	11.200	4.200	3.800	1.800	5.000	6.400	
POST ORB	7.900	9.600	10.500	11.200	13.100	11.400	2.100	14.400	1.400	
ZYGO BR	2.300	6.200	5.600	6.300	12.900	11.400		12.100	2.300	
BCASE BR	2.700	6.300	5.600	6.600	17.600	7.400		12.900		
MASTOIDB		0.800	0.700	0.600	7.300	6.800		9.700		
PALATE L		2.200	1.600	1.700	7.400	0.800		8.100		
BCASE HT			1.800	2.200	0.900	2.000		1.100		
MTR					2.200	2.200		2.200		
M3 LENG					2.700			2.800		
M3 WIDTH										
C1 C1										

	M ATERA	M BONDA	M COIBEA	M MOLOSS	M PRETIA	M SINALA	M TRINIA	MYOP ALB	MYOP WHA	NEOPLATA
M3 M3	6.600	5.000	4.600	4.600	5.600	5.000	4.800	6.800	5.100	3.300
ANT PTER	2.800	2.400	2.100	2.600	2.600	2.200	2.200	2.500	2.400	1.600
POSTPTER	3.000	2.400	2.200	2.700	3.000	2.600	2.200	2.600	1.500	2.000
LO CANIN	3.400	3.100	2.200	2.100	3.000	3.400	3.200	4.100	2.000	2.000
DENT LEN	15.600	10.700	11.200	12.100	14.400	13.300	12.900	17.100	11.800	10.200
FOR ANT	13.400	3.400	9.500	10.200	22.000	11.400	2.900	14.700	14.000	8.500
ANGUL L	3.700	3.700	2.800	3.000	4.000	3.500	1.420	5.700	2.800	2.400
CON CORO	5.200	9.800	3.700	4.100	4.800	4.100	4.000	5.700	2.800	3.300
COND M1	12.200	3.200	8.700	9.300	11.100	10.400	9.900	13.400	9.300	7.700
ANGUL W	4.300	9.000	2.600	3.300	4.500	3.600	3.400	3.800	2.200	2.000
CORO MT	5.100	3.000	3.600	3.900	4.600	4.400	3.600	6.600	4.000	3.400
INCI FOR	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
N SHAPE	1.000	1.000	6.000	6.000	6.000	6.000	5.000	5.000	5.000	1.000
PREMOLAR	6.000	3.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000
BASI PIT	1.000	3.000	1.000	3.000	3.000	3.000	4.000	4.000	4.000	2.000
A SAGITT	3.000	1.000	3.000	2.000	3.000	3.000	3.000	1.000	1.000	1.000
P SAGITT	3.000	1.000	3.000	1.000	1.000	3.000	2.000	1.000	1.000	1.000
EAR JUNC	2.000	2.200	2.000	2.000	2.000	2.000	1.000	1.000	1.000	2.000
WRINKLES	1.000	1.600	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
M1 META	1.000	3.000	1.800	1.700	2.200	1.900	1.800	2.300	1.600	1.420
GLENO L	2.600	3.000	2.000	1.600	2.000	2.400	2.200	2.700	1.500	1.200
GLENO W	2.800	3.000	1.600	1.400	2.600	1.700	1.600	2.100	1.400	1.200
UP MOL R	2.200	2.200	4.000	4.000	2.000	5.600	5.430	7.100	5.000	4.000
CONDY L	1.600	1.600	1.600	1.600	5.800	3.000	3.000	3.000	3.000	3.000
HAIRYNES	3.000	3.000	3.000	3.000	3.000	3.000	3.000	2.000	3.000	3.000
L LAMBDO	3.000	3.000	2.000	3.000	3.000	3.000	2.000	2.000	2.000	3.000
S LAMBDO	3.000	2.000	3.000	3.000	3.000	3.000	3.000	2.000	2.000	3.000
DIGIT 3	100.000	76.900	69.700	77.400	90.700	91.200	87.800	108.800	70.500	54.900
DIGIT 4	74.400	58.300	52.000	57.400	66.700	67.200	65.700	85.700	58.600	45.300
DIGIT 5	52.800	41.800	35.700	41.500	45.900	49.200	46.600	60.300	39.800	33.600
ASPECT	2.854	2.859	2.899	2.786	2.996	2.813	2.820	2.697	2.641	2.485
TIP INDX	66.360	66.860	67.340	66.615	65.820	65.900	66.820	67.080	62.641	65.750
D3 I D5	1.894	1.911	1.952	1.855	1.972	1.854	0.884	1.804	1.771	1.634
EAR I FA	0.325	0.328	0.379	0.313	0.277	0.271	0.0	0.409	0.376	0.430
CONMT DL	0.128	0.143	0.143	0.107	0.125	0.113	0.132	0.140	0.136	0.186
DTHIC DL	0.141	0.143	0.143	0.149	0.139	0.150	0.147	0.129	0.102	0.118
MI+M2 DL	0.647	0.619	0.625	0.661	0.653	0.624	0.612	0.673	0.568	0.549
COR H DL	0.327	0.317	0.313	0.322	0.319	0.331	0.279	0.386	0.339	0.333

	OTO MARA	OTO PAPU	OTO SECA	OTO WROA	PLATYMOA	PRO CEN	PRO NASU	SAUROMYS	MIMETILL	NYCTALUS
HEAD BOD	100.000	0.0	72.000	90.000	61.000	81.500	68.000	67.000	60.000	83.000
TAIL	45.000	20.000	35.500	43.000	30.500	51.500	52.000	41.000	32.000	53.000
EAR	40.500	10.000	25.000	33.000	15.000	15.500	13.000	17.000	13.000	17.500
HF	12.600	13.600	9.000	12.500	7.000	9.600	10.600	7.200	6.600	12.000
TIBIA	18.600	50.800	14.000	16.400	8.300	17.600	16.300	10.300	9.500	16.500
FOREARM	67.200	18.800	56.400	66.500	33.700	52.600	48.400	40.300	29.500	50.500
3H META	70.200	16.900	57.400	24.600	33.700	56.200	51.800	42.400	30.500	50.400
3H 1PHAL	24.200	47.200	20.300	24.200	14.200	25.600	21.800	16.200	7.500	19.300
3H 2PHAL	26.200	11.700	53.100	62.000	12.300	21.600	19.800	13.900	7.500	13.200
4 META	65.000	8.500	12.900	16.600	33.000	54.200	50.200	41.000	29.900	49.500
4H 1PHAL	17.000	25.300	8.600	12.600	12.600	21.500	18.100	14.200	8.600	17.500
4H 2PHAL	12.200	15.800	27.900	32.700	9.200	33.800	3.100	7.100	1.500	6.900
5H META	35.400	5.100	17.800	21.600	25.600	14.200	34.200	28.100	26.500	39.900
5H 1PHAL	21.800	19.700	7.800	9.900	6.800	8.800	13.700	11.200	2.200	9.400
5H 2PT1P	10.800	17.800	5.600	6.900	8.600	5.000	5.400	6.100	1.600	5.800
5H T1P	5.800	8.100	2.600	6.000	2.400	20.000	3.200	17.600	15.100	11.900
UP CANIN	3.800	6.300	21.300	24.400	15.500	19.400	17.700	17.800	15.700	18.500
GSL	27.300	5.100	19.300	29.800	6.500	7.600	6.500	7.800	5.700	19.300
CON INCI	25.300	12.100	6.200	7.600	5.800	6.500	5.800	5.800	7.400	8.000
ROST LEN	12.000	1.300	4.200	6.100	5.600	13.200	4.400	12.000	10.300	8.700
LACR WID	8.100	1.300	12.900	19.100	16.200	8.200	17.100	6.900	1.500	13.500
INTORB W	6.100	3.400	0.900	0.800	1.700	1.800	1.600	1.500	1.400	7.500
COA CAN1	18.400	4.400	1.200	1.400	3.600	1.800	1.400	1.400	3.400	2.300
LOWER TR	10.400	10.500	4.000	4.800	3.800	3.800	3.200	3.700	2.500	1.700
TR CON H	1.600	10.600	3.400	3.200	3.800	3.400	3.530	3.800	5.100	3.200
DENTTHIC	5.200	7.300	5.400	15.200	11.800	4.200	4.000	11.500	8.200	5.400
MOM1 COR	4.400	7.400	10.200	11.600	8.600	12.600	9.400	9.200	10.900	13.200
MOM2 ANG	5.400	1.200	11.200	12.600	7.600	10.200	6.800	11.100	5.100	10.200
POST ORB	14.200	2.000	7.500	8.800	5.400	11.800	6.300	4.700	1.600	12.600
ZYGO BR	12.200		1.200	1.400	1.800	8.000	0.700	6.900	3.390	6.700
BCASE BR	13.700		1.600	3.000	2.500	1.000	1.900	0.900		7.100
MASTOIDB	10.700		2.400			2.200	1.600	2.700		1.200
PALATE L	8.400									2.300
BCASE HT	10.700									4.300
MTR	1.500									
M3 LENG	2.200									
M3 WIDTH	3.000									
CI CI										

148

	OTO MARA	OTO PAPU	OTO SECA	OTO WROA	PLATYWOA	PRO CEN	PRO NASU	SAUROMYS	MIMETILL	NYCTALUS
M3 M3	6.100	4.400	4.600	5.700	4.000	5.600	4.900	3.900	4.200	4.900
ANT PTER	4.000	4.000	3.000	2.900	1.900	2.800	2.300	2.200	2.200	2.700
POSTPTER	3.400	2.400	2.800	2.900	2.400	2.600	2.600	2.200	2.130	3.000
LO CANIN	3.600	2.700	2.500	3.400	2.100	3.400	3.000	2.000	2.100	3.000
DENT LEN	18.600	12.400	13.400	15.600	11.400	13.600	11.600	16.400	11.100	14.600
FOR ANT	16.200	10.900	12.200	13.900	9.500	11.400	9.700	16.200	9.000	11.600
ANGUL L	3.400	2.600	2.200	2.800	2.800	3.600	3.400	2.800	2.700	3.300
CON CORO	5.200	3.600	3.900	4.300	3.800	3.900	3.400	3.900	3.400	4.600
COND MI	13.200	8.800	9.700	11.300	8.900	10.200	8.800	9.900	8.500	11.800
ANGUL W	3.400	2.800	2.700	3.000	2.800	3.900	2.600	1.700	1.600	2.600
CORO HT	3.500	2.900	2.400	3.200	4.400	5.000	3.600	4.000	5.000	5.000
INCI FOR	3.000	3.000	3.000	3.000	3.000	3.000	1.000	2.000	1.000	3.000
N SHAPE	1.000	1.000	1.000	1.000	1.000	2.000	1.000	2.000	1.000	1.000
PREVCLAR	4.000	4.000	4.000	4.000	1.000	2.000	1.000	2.000	1.000	1.000
BASI PIT	5.000	5.000	5.000	5.000	1.000	2.000	1.000	1.000	1.000	1.000
A SAGITT	2.000	3.000	1.000	1.000	1.000	2.000	1.000	2.000	1.000	1.000
P SAGITT	3.000	3.000	3.000	3.000	1.000	1.000	1.000	3.000	3.000	1.000
EAR JUNC	4.000	4.000	4.000	4.000	1.400	2.400	1.700	1.400	1.300	1.900
WRINKLES	2.200	1.700	1.600	2.300	1.000	1.820	1.200	1.300	1.200	2.200
MI META	1.800	1.800	1.800	1.800	1.600	1.800	1.500	1.800	1.700	1.900
GLENO L	7.200	5.200	5.000	6.400	1.300	3.600	1.800	1.300	1.400	5.700
GLENO W	1.200	1.600	1.400	1.000	4.700	3.000	5.000	4.700	4.000	1.000
CONDY L	2.000	2.000	2.000	2.000	3.000	3.000	3.000	2.000	1.000	2.000
UP MOL R	1.000	1.000	1.000	1.000	2.000	1.000	1.000	3.000	1.000	2.000
HAIRYNES	1.000	1.000	1.000	1.000	2.000	1.000	1.000	3.000	1.000	2.000
L LAMBDO	2.000	2.000	1.000	1.000	2.000	1.000	1.030	3.000	48.000	2.000
S LAMBDO	1.000	1.000	1.000	1.000	2.000	1.000	1.000	3.000	48.000	2.000
DIGIT 3	126.400	91.600	103.400	121.300	66.900	107.800	98.400	78.600	48.600	94.800
DIGIT 4	94.200	67.400	74.500	90.100	55.200	79.100	72.400	62.300	40.300	74.600
DIGIT 5	68.000	48.600	53.500	64.200	41.200	56.800	55.700	46.500	32.400	55.100
ASPECT	2.847	2.895	2.994	2.893	2.415	2.824	2.636	2.557	2.410	2.637
TIP INDX	65.190	64.960	64.540	65.320	66.670	67.216	67.030	66.110	62.233	65.240
D3 I D5	1.859	1.881	1.933	1.889	1.610	1.898	1.767	1.690	1.500	1.721
EAR I FA	0.603	0.405	0.440	0.520	0.470	0.295	0.269	0.422	0.441	0.337
CONHT DL	0.054	0.097	0.067	0.051	0.149	0.132	0.138	0.121	0.171	0.158
DTHIC DL	0.086	0.105	0.090	0.090	0.105	0.118	0.121	0.097	0.099	0.116
M1+M2 DL	0.505	0.540	0.522	0.526	0.596	0.603	0.578	0.548	0.532	0.541
COR H DL	0.188	0.234	0.179	0.205	0.386	0.287	0.310	0.331	0.360	0.308

APPENDIX B

SUMMARY OF NAMES FOR MOLOSSID BATS

(compiled from the literature)

Family **MOLOSSIDAE**

Molossi Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 258.

Molossidae Gill, 1872, Arrangement of the families of mammals, p. 17 (=*Molossina* Gervais, 1855, Exped. du Comte de Castelnau. Zool., Mamm., p. 52; see Miller, 1907, for additional details).

Allomops see *Mops*

Austronomus see *Tadarida*

Cephalotes see *Tadarida*

Chaerephon Dobson

Chaerephon Dobson, 1874, J. Asiatic Soc. Bengal, **43**, pt. 2, p. 144 (subgenus of *Nyctinomus*; type *Nyctinomus johorensis*).

Chaerephon: Andersen, 1907, Ann. Mus. Civ. Stor. Nat. Genova, ser. 3, **3**, p. 35 (genus).

Lophomops J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 460 (subgenus of *Chaerephon*).

Chaerephon: Ellerman and Morrison-Scott, 1951, Checklist of Palaearctic and Indian Mammals 1758 to 1946, London, British Museum (Nat. Hist.), p. 135 (subgenus of *Tadarida*).

Chaerephon aloysiisabaudiae (Festa)

Nyctinomus AloysiiSabaudiae Festa, 1907, Boll. Mus. Zool. Anat. Comp., **22**, pt. 546, p. 1–2.

Tadarida (Chaerephon) aloysiisabaudiae: Lanza and Harrison, 1963, Z. Säugetierk., **28**, p. 106.

Tadarida cyclotis Brosset, 1966, Biol. Gabonica, **11**, p. 80.

Tadarida brunnea: Hayman, Misonne and Verheyen, 1966, Ann. Mus. Roy. African Cent., Ser. Zool. 154, p. 67 (type of *T. brunnea* assigned to *T. aegyptiaca*, Peterson, 1972).

Chaerephon ansorgei (Thomas)[1]

Nyctinomus ansorgei Thomas, 1913, Ann. Mag. Nat. Hist., ser. 8, **11**, p. 318.

Nyctinomus rhodesiae Roberts, 1946, Ann. Transv. Mus., **20**, p. 307.

Chaerephon bemmelini (Jentinck)

Nyctinomus bemmelini Jentinck, 1879, Notes Roy. Zool. Mus. Netherlands at Leiden, **1**, p. 125.

Nyctinomus cisturus Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, **12**, p. 502.

---

[1]No previous author has put *ansorgei* into *Chaerephon*, but my analysis supports this change and K. F. Koopman agrees with me.

Chaerephon bivittata (Heuglin)

Nyctinomus bivittatus Heuglin, 1861, Novorum Actorum Acad. Caesareae Leopoldino-Carolinae, **29**, no. 8, pp. 4, 13.

Chaerephon chapini J. A. Allen

Chaerephon (Lophomops) chapini J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 461.

Chaerephon (Lophomops) shortridgei Thomas, 1926, Proc. Zool. Soc. London, **1926**, p. 289 (valid as a subspecies).

Chaerephon lancasteri Hayman, 1938, Ann. Mag. Nat. Hist. ser. 11, **1**, p. 383 (valid as a subspecies).

Chaerephon gallagheri (Harrison)[2]

Tadarida (Chaerephon) gallagheri Harrison, 1975, Mammalia, **39**, p. 313.

Chaerephon jobensis (Miller)

Nyctinomus jobensis Miller, 1902, Proc. Biol. Soc. Washington, **15**, p. 246.

Nyctinomus plicatus colonicus Thomas, 1906, Proc. Zool. Soc. London, **1906**, p. 537 (subspecies is *Chaerephon jobensis colonicus*).

Chaerephon solomonis Troughton, 1931, Proc. Linn. Soc. New South Wales, **56**, p. 207 (valid as a subspecies).

Tadarida jobensis bregullae Felten, 1964, Senckenbergiana Biol., **45**, p. 9.

Chaerephon johorensis (Dobson)

Molossus (Nyctinomus) johorensis Dobson, 1873, Proc. Asiatic Soc. Bengal, p. 22.

Chaerephon major (Trouessart)

Nyctinomus pumilus var. *major* Trouessart, 1897, Catalogus mammalium tam viventium quam fossilum. 2nd ed. Berlin, **1**, p. 146.

Nyctinomus emini De Winton, 1901, Ann. Mag. Nat. Hist., ser. 7, **7**, p. 40.

Chaerephon (Lophomops) abae J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 464.

Tadarida (Chaerephon) pumila: Happold, 1967, Sudan Notes Rec., **48**, p. 122 (different from *Dysopes pumilus* Cretzschmar).

Chaerephon nigeriae Thomas

Chaerephon nigeriae Thomas, 1913, Ann. Mag. Nat. Hist., ser. 8, **11**, p. 319.

Nyctinomus spillmani Monard, 1933, Bull. Soc. Sci. Nat., Neuchâtel, **57**, p. 51 (valid as a subspecies).

Chaerephon plicata (Buchannan)

Vespertilio plicatus Buchannan, 1800, Trans. Linn. Soc. London, **5**, p. 261, pl. 13.

Nyctinomus bengalensis Desmarest, 1820, Encyclop. Méth. (Mamm.), **1**, p. 116.

Nyctinomus dilatatus Horsfield, 1822, Zool. Res. Java, pl. Java (valid as a subspecies).

Nyctinomus tenuis Horsfield, 1822, Zool. Res. Java, pl. Proewoto (valid as a subspecies).

[2]Not included in my study.

Dysopes murinus Gray, 1830, Illus. Index Zool., pt. 3, pl. 1.

Chaerephon luzonus Hollister, 1913, Proc. U.S. Nat. Mus., **45,** p. 312 (valid as a subspecies).

Chaerephon plicatus insularis Phillips, 1932, Spolia Zeylan, **16,** p. 334.

Chaerephon plicatus adustus Sody, 1936, Naturk. Tijdschr. Ned.-Ind., **96,** p. 50 (synonym of *C. p. tenuis*).

Chaerephon pumila (Cretzschmar)

Dysopes pumilus Cretzschmar, 1826 [1826–1830], Säugetiere, *in* Senckenbergische naturforschende Gesellschaft: Atlas zu der Reise in nordlichen Afrika von Eduard Rüppell. Frankfurt am Main, p. 69, pl. 27.

Dysopes limbatus Peters, 1852, Reise nach Mossambique, Säugeth., p. 56, pl. 54 (valid as a subspecies).

Dysopes dubius Peters, 1852, Reise nach Mossambique, Säugeth., p. 60, pl. 15, f. 2 (*C. p. limbatus?; not of A. Smith, 1833).

Nyctinomus leucogaster A. Grandidier, 1869, Rev. Mag. Zool., ser. 2, **21,** p. 337.

Nyctinomus gambianus De Winton, 1901, Ann. Mag. Nat. Hist., ser. 7, **7,** p. 39.

Nyctinomus pusillus Miller, 1902, Proc. Biol. Soc. Washington, **15,** p. 245.

Nyctinomus hindei Thomas, 1904, Ann. Mag. Nat. Hist., ser. 7, **13,** p. 210 (valid as a subspecies).

Chaerephon websteri Dollman, 1908, Ann. Mag. Nat. Hist., ser. 8, **2,** p. 546 (possibly valid as a subspecies).

Chaerephon pumilus naivashae Hollister, 1916, Smithsonian Misc. Coll., **6,** no. 1, p. 4 (synonym of *C. p. hindei*).

Chaerephon frater J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37,** p. 456 (possibly valid as a subspecies).

Chaerephon (Lophomops) cristatus J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37,** p. 463.

Chaerophon pumilus elphicki Roberts, 1926, Ann. Transvaal Mus., **11,** p. 245 (valid as a subspecies).

Chaerophon (Lophomops) nigri Hatt, 1928, Bull. Soc. Zool. de France, **53,** p. 374.

Chaerephon (Lophomops) langi Roberts, 1932, Ann. Transvaal Mus., **15,** p. 17 (valid as a subspecies).

Tadarida (Chaerephon) faini Hayman, 1951, Rev. Zool. Bot. Africaines, **45,** p. 82 (possibly valid as a subspecies).

Chaerephon russata J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37,** p. 458.

Cheiromeles Horsfield

Cheiromeles Horsfield, 1924, Zool. Res. Java, pt. 8.

Chiropetes Gloger, 1841, Gemeinnutziges Hand-u. Hilfsbuch der Naturg., **1,** p. 49.

Cheiromeles parvidens Miller and Hollister

Cheiromeles parvidens Miller and Hollister, 1921, Proc. Biol. Soc. Washington, **34,** p. 100.

Cheiromeles torquatus Horsfield

Cheiromeles torquatus Horsfield, 1824, Zool. Res. Java, pt. 8.

Dysopes cheiropus Temminck, 1826, Monogr. Mammal., **1,** p. 218.

Cheiromeles caudatus Temminck, 1841, Monogr. Mammal., **2**, p. 348 (valid as a subspecies).

Cheiromeles jacobsoni Thomas, 1923, Ann. Mag. Nat. Hist., ser. 9, **12,** p. 592 (valid as a subspecies).

Cynomops see *Molossops*

Dinops see *Tadarida*

Dysopes see *Tadarida, Molossops, Eumops, Molossus*

Eomops see *Myopterus*

Eumops Miller[3]

Vespertilio: Shaw, 1800, General Zoology, Mammalia, **1,** pt. 1, p. 137 (not Linnaeus, 1758).

Molossus: Schinz, 1821, Das Thierreich, **1,** p. 870 (not Geoffroy, 1805).

Dysopes: Wied, 1826, Beitr. Naturg. Brasil., **2,** p. 226 (not Illiger, 1811).

Promops: Peters, 1874, Monatsber. K. Preuss. Akad. Wiss. Berlin, **1874,** p. 232; Dobson, 1878, Catalog of the Chiroptera in the British Museum, p. 414 (not Gervais, 1855).

Eumops Miller, 1906, Proc. Biol. Soc. Washington, **19,** p. 85.

Eumops auripendulus (Shaw)

Vespertilio auripendulus Shaw, 1800, General Zoology, Mammalia, **1,** pt. 1, p. 137.

Molossus rufus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, **6,** p. 155.

Molossus amplexi-caudatus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, **6,** p. 156.

Dysopes longimanus Wagner, 1843, Arch. Naturg., **9,** pt. 1, p. 367.

Dysopes leucopleura Wagner, 1843, Arch. Naturg., **9,** pt. 1, p. 367.

Molossus nasutus: J. A. Allen, 1897, Bull. Amer. Mus. Nat. Hist., **9,** p. 115 (not Spix, 1823).

Promops milleri J. A. Allen, 1900, Bull. Amer. Mus. Nat. Hist., **13,** p. 92.

Promops barbatus J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., **20,** p. 228.

Eumops abrasus: Miller, 1906, Proc. Biol. Soc. Washington, **19,** p. 85 (not Temminck, 1827).

Eumops maurus: Villa-R, 1956, An. Inst. Biol. Mexico, **26,** p. 543 (not Thomas, 1901).

Eumops auripendulus: Goodwin, 1960, Amer. Mus. Novitates, **1994,** p. 5.

Eumops auripendulus major Eger, 1974, Life Sci. Occas. Pap. Roy. Ontario Mus., **25,** p. 2.

Eumops bonariensis (Peters)

Promops bonariensis Peters, 1874, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 232–234.

Molossus bonariensis: Dobson, 1876, Proc. Zool. Soc. London, **1876,** p. 715.

---

[3]Details in Eger, 1977.

Promops nanus Miller, 1900, Ann. Mag. Nat. Hist., ser. 7, **6**, p. 470 (valid as a subspecies).

Eumops bonariensis: Miller, 1906, Proc. Biol. Soc. Washington, **19**, p. 85.

Eumops delticus Thomas, 1923, Ann. Mag. Nat. Hist., ser. 12, **9**, p. 341 (valid as a subspecies).

Eumops patagonicus Thomas, 1924, Ann. Mag. Nat. Hist., ser. 9, **13**, p. 234.

Eumops bonariensis becheri Sanborn, 1932, J. Mammal., **13**, p. 355.

Eumops dabbenei Thomas[4]

Eumops dabbenei Thomas, 1914, Ann. Mag. Nat. Hist., ser. 8, **13**, p. 481.

Eumops perotis dabbenei Sanborn, 1932, J. Mammal., **13**, p. 350.

Eumops glaucinus (Wagner)

Dysopes glaucinus Wagner, 1843, Arch. Naturg., **9**, pt. 1, p. 368.

Molossus ferox Gundlach, 1861, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 149.

Molossus glaucinus: Dobson, 1876, Proc. Zool. Soc. London, **1876**, p. 714.

Nyctinomus orthotis H. Allen, 1889, Proc. Amer. Philos. Soc., **26**, p. 561.

Promops glaucinus: Miller, 1900, Ann. Mag. Nat. Hist., ser. 7, **6**, p. 471.

Eumops glaucinus: Miller, 1906, Proc. Biol. Soc. Washington, **19**, p. 85.

Molossides floridanus G. M. Allen, 1932, J. Mammal., **13**, p. 257 (valid as a subspecies).

Eumops floridanus: Ray, Olsen, and Gut, 1963, J. Mammal., **44**, p. 377.

Eumops hansae Sanborn

Eumops hansae Sanborn, 1932, J. Mammal., **13**, p. 356.

Eumops amazonicus Handley, 1955, Proc. Biol. Soc. Washington, **68**, p. 177.

Eumops maurus (Thomas)

Molossus maurus Thomas, 1901, Ann. Mag. Nat. Hist., ser. 8, **7**, p. 141.

Myopterus maurus: Trouessart, 1904, Cat. Mamm., Suppl., p. 101.

Eumops maurus: Miller, 1906, Proc. Biol. Soc. Washington, **19**, p. 85.

Eumops geijskesi Husson, 1962, Bats of the Suriname, E. J. Brill, Leiden, p. 246.

Eumops perotis (Schinz)

Molossus perotis Schinz, 1821, Das Thierreich, **1**, p. 870.

Dysopes perotis: Wied, 1827, Beitr. Naturg. Brasil, **2**, p. 227.

Dysopes (Molossus) gigas Peters, 1864, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 381.

Molossus californicus Merriam, 1890, N. Amer. Fauna, **4**, p. 31 (valid as a subspecies).

Promops trumbulli Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, **7**, p. 190.[5]

Promops perotis: Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, **7**, p. 191.

Eumops perotis: Miller, 1906, Proc. Biol. Soc. Washington, **19**, p. 85.

Eumops perotis renatae Pirlot, 1965, Nat. Canadien, **92**, p. 5.

---

[4]Not included in my study.

[5]Eger, 1977, considered it a full species, but specimens of *trumbulli* from AMNH which I had in my larger analysis placed so close to *E. perotis* that I did not feel justified in using it in the final analysis. Koopman (1978) considered *trumbulli* a subspecies of *perotis*.

Eumops underwoodi Goodwin

Eumops underwoodi Goodwin, 1940, Amer. Mus. Novitates, **1075**, p. 2.
Eumops sonoriensis Benson, 1947, Proc. Biol. Soc. Washington, **60**, p. 133 (valid as a subspecies).
Eumops underwoodi mederai Massoia, 1976, Physis, C, **35**, p. 264.

Lophomops see *Chaerephon*

Micronomus see *Mormopterus*

Molossops Peters

Dysopes: Burmeister, 1854, Syst. Uebers. Thiere Brasil, p. 72 (not Illiger, 1811).
Molossops Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575 (subgenus of *Molossus*).
Myopterus Peters, 1869, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 402 (not *Myopterus* Geoffroy, 1813).
Molossops: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 247.
Cynomops Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, **5**, p. 189.

Molossops (Cynomops) brachymeles (Peters)

Molossus (Molossops) brachymeles Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575.
Molossus cerastes Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, **8**, p. 199 (valid as a subspecies).
Molossops mastivus Thomas, 1911, Ann. Mag. Nat. Hist., ser. 8, **7**, p. 113 (valid as a subspecies).
Molossops brachymeles: Thomas, 1911, Ann. Mag. Nat. Hist., ser. 8, **7**, p. 114.
Cynomops cerastes: Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, **5**, p. 189.
Molossops (Cynomops) brachymeles: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, pp. 118–119.

Molossops (Cynomops) greenhalli (Goodwin)

Cynomops greenhalli Goodwin, 1958, Amer. Mus. Novitates, **1877**, pp. 3–5.

Molossops (Cynomops) planirostris (Peters)

Molossus planirostris Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575.
Molossus planirostris paranus Thomas, 1901, Ann. Mag. Nat. Hist., ser. 7, **8**, p. 190.
Promops nanus Bangs, 1906, Bull. Mus. Comp. Zool., **46**, p. 212 (not Miller, 1900).
Molossops milleri Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10**, p. 183 (valid as a subspecies, see Koopman, 1978).
Cynomops planirostris: Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, **5**, p. 189.
Molossops (Cynomops) planirostris: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 119.

Molossops (Molossops) aequatorianus Cabrera[6]

Molossus nasutus Cabrera, 1901, Bol. Soc. Espan. Hist. Nat., **1**, p. 370 (not Spix, 1823).

Molossops aequatorianus Cabrera, 1917, Trab. Mus. Nac. Cienc. Nat., Zool., **31**, p. 20.

Molossops (Molossops) aequatorianus: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 117.

Molossops (Molossops) temminckii (Burmeister)

Dysopes temminckii Burmeister, 1854, Syst. Uebers. Thiere Brasil., p. 72.

Molossus (Molossops) temminckii: Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 575.

Molossus hirtipes Winge, 1892, E. Mus. Lundii., p. 17.

Molossops temminckii: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 248.

Molossops temminckii sylvia Thomas, 1924, Ann. Mag. Nat. Hist., ser. 9, **13**, p. 235.

Molossops temminckii griseiventer Sanborn, 1941, Field Mus. Nat. Hist., Zool. Ser., **27**, p. 385.

Molossops (Molossops) temminckii: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 118.

Molossops (Neoplatymops) mattogrossensis Vieira

Molossops mattogrossensis Vieira, 1942, Arg. Zool. São Paolo, **3**, p. 430.

Molossops temminckii mattogrossensis: Cabrera, 1957, Rev. Mus. Argentino Cienc. Nat., Cien. Zool., **4**, p. 117.

Cynomops mattogrossensis: Goodwin, 1958, Amer. Mus. Novitates, **1877**, p. 5.

Neoplatymops mattogrossensis: Peterson, 1965, Life Sci. Contrib. Roy. Ontario Mus., **64**, p. 3.

Molossus Geoffroy

Molossus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, **6**, p. 151.

Dysopes Illiger, 1811, Prodromus systematis mammalium et avium, p. 76.

Molossus ater Geoffroy

Molossus ater Geoffroy, 1805, Bull. Sci. Soc. Philom., **3**, no. 96, p. 279; Ann. Mus. Hist. Nat. Paris, **6**, p. 155.

Molossus castaneus Geoffroy, 1805, Ann. Mus. Hist. Nat. Paris, **6**, p. 155.

Molossus ursinus Spix, 1823, Sim. et Vespert. Brasil, p. 59.

Dysopes alecto Temminck, 1827, Monogr. Mammal., **1**, p. 231.

Dysopes holosericeus Wagner, 1843, Arch. Naturg., **9**, pt. 1, p. 368.

Dysopes albus Wagner, 1843, Arch. Naturg., **9**, pt. 1, p. 368.

Molossus myosurus Tschudi, 1844–46, Fauna Peruana, Mamm., p. 83.

Molossus rufus: Dobson, 1876, Proc. Zool. Soc. London, **1876**, p. 710 (not Geoffroy, 1805).

Molossus fluminensis Lataste, 1891, Ann. Mus. Civ. Stor. Nat., Genova, ser. 2, **10**, p. 658.

[6]Not included in my study.

Molossus nigricans Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54**, p. 395 (valid as a subspecies).

Cynomops malagai Villa-R., 1955, Acta Zool. Mexicana, **1**, no. 4, p. 2.

Molossus bondae J. A. Allen

Molossus bondae J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., **20**, p. 228.

Molossus coibensis J. A. Allen[7]

Molossus coibensis J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., **20**, p. 227.

Molossus macdougalli Goodwin[8]

Molossus pretiosus macdougalli Goodwin, 1956, Amer. Mus. Novitates, **1757**, p. 3.

Molossus macdougalli Goodwin, 1969, Bull. Amer. Mus. Nat. Hist., **141**, p. 114 (also earlier Goodwin, 1964, Amer. Mus. Novitates, **2195**, p. 20).

Molossus molossus (Pallas)

V(espertilio) Molossus (part) Pallas, 1766, Miscellanea zoologica, pp. 45–50.

Vespertilio molossus major Kerr, 1792, Animal Kingdom, p. 97.

Vespertilio molossus minor Kerr, 1792, Animal Kingdom, p. 97.

Molossus obscurus Geoffroy, 1805, Bull. Sci. Philom. Paris, **3**, no. 96, p. 279.

Molossus longicaudatus Geoffroy, 1805, Bull. Sci. Philom. Paris, **3**, no. 96, p. 279.

Molossus fusciventer Geoffroy, 1805, Bull. Sci. Philom. Paris, **3**, no. 96, p. 279.

Molossus crassicaudatus Geoffroy, 1805, Ann. Mag. Hist. Nat. Paris, **6**, p. 156 (valid as a subspecies).

Molossus acuticaudatus Desmarest, 1820, Mammalogie (Brazil), p. 116.

Dysopes velox Temminck, 1827, Monogr. Mammal., **1**, p. 234.

Molossus moxensis D'Orbigny, 1835, Voy. Amer. Merid., Atlas Zool., lam. **11**, figs. 1–4.

Molossus fuliginosis Gray, 1838, Mag. Zool. and Bot., **2**, p. 501 (not Cooper, 1837).

Molossus tropidorhynchus Gray, 1839, Ann. Mag. Nat. Hist., ser. 11, **4**, p. 6 (possibly valid as a subspecies; K. F. Koopman, *in verbis*).

Dysopes fumarius Schinz, 1844, Syst. Verz. Säug., **1**, p. 114 (not Spix, 1823).

Dysopes olivaceofuscus Wagner, 1850, Abhandl. Bayer. Akad. Wiss., **5**, p. 202.

Dysopes amplexicaudatus Wagner, 1850, Abhandl. Bayer. Akad. Wiss., **5**, p. 202.

M(olossus) aztecus Saussure, 1860, Rev. et. Mag. Zool., Paris, ser. 2, **12**, p. 285 (valid as a subspecies; Gardner, 1966, L. A. County Mus. Nat. Hist. Contrib. in Sci., no. 111, pp. 1–6, reported a full species).

[7] I strongly believe that *M. coibensis* is not a full species. It is more likely a subspecies of *M. molossus* or *M. bondae*. Hall & Kelson (1959) and K. F. Koopman (personal communication) allied *coibensis* with *molossus*, but my analysis places *coibensis* closer to *bondae*.

[8] This taxon was overlooked as a species in my analysis. Hall & Kelson (1959) listed it as a subspecies of *pretiosus*. Specimens of *macdougalli* at AMNH have little development of the sagittal crest. Until a more complete study of the larger forms of *Molossus* is done, I believe I can only report *macdougalli* as it is in the literature right now, i.e., as a full species.

Molossus pygmaeus Miller, 1900, Proc. Biol. Soc. Washington, **13,** p. 162 (possibly valid as a subspecies).

Molossus burnesi Thomas, 1905, Ann. Mag. Nat. Hist., ser. 7, **15,** p. 584.

Molossus verrilli J. A. Allen, 1908, Bull. Amer. Mus. Nat. Hist., **24,** p. 581 (possibly valid as a subspecies).

Molossus currentium: Miller, 1913, Proc. U.S. Nat. Mus., **46,** p. 89.

Molossus fortis Miller, 1913, Proc. U.S. Nat. Mus., **46,** p. 89 (valid as a subspecies).

Molossus debilis, Miller, 1913, Proc. U.S. Nat. Mus., **46,** p. 90 (valid as a subspecies).

Molossus cherriei J. A. Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35,** p. 529.

Molossus daulensis J. A. Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35,** p. 530 (valid as a subspecies).

Molossus milleri Johnson, 1952, Proc. Biol. Soc. Washington, **65,** p. 197 (possibly valid as a subspecies; K. F. Koopman, *in verbis*).

Molossops planirostris espiritosantensis Ruschi, 1951, Bol. Mus. Biol. Prof. Mello-Leitão Zool., Santa Teresa, Espírito Santo, no. 6, p. 2 (synonymous with *Molossus molossus crassicaudatus*).

Molossus pretiosus Miller

Molossus pretiosus Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54,** p. 396.

Molossus sinaloae J. A. Allen

Molossus sinaloae J. A. Allen, 1906, Bull. Amer. Mus. Nat. Hist., **22,** p. 236.

Molossus trinitatus Goodwin[9]

Molossus trinitatus Goodwin, 1959, Amer. Mus. Novitates, **1967,** p. 1.

Mops Lesson

Mops Lesson, 1842, Nouv. Table. Règne Animal, Mamm., p. 18 (Genotype *Mops indicus* Lesson = *Dysopes mops* F. Cuvier; listed in synonymy of *Nyctinomus* by Miller, 1907, Bull. U.S. Nat. Mus., **57,** p. 251; but listed as a genus with distinct characters by Thomas, 1913, J. Bombay Nat. Hist. Soc., **22,** p. 91).

Allomops J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37,** p. 470 (given as a subgenus of *Mops*).

Philippinopterus Taylor, 1934, Philippine land mammals, p. 314.

Tadarida (Mops) Ellerman and Morrison-Scott, 1951, Checklist of Palaearctic and Indian Mammals, 1758 to 1946, p. 133.

Mops brachyptera (Peters)

Dysopes brachypterus Peters, 1852, Reise nach Mossambique, Säugeth., p. 59, pl. 15, f. 1.

Mops condylura (A. Smith)

Nyctinomus condylurus A. Smith, 1833, South African Quart. J., **1,** p. 54.

---

[9]Ojasti & Linares (1971) thought *M. trinitatus* was a subspecies of *M. sinaloae*. My analysis shows *trinitatus* to be different from other species of *Molossus* (see text for details).

Nyctinomus angolensis Peters, 1870, J. Sci. Math. Phys. Nat. Lisboa, ser. 1, **3**, p. 124.

Mops (*Allomops*) *osborni* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 473 (possibly valid as a subspecies).

Chaerephon leucostigma G. M. Allen, 1918, Bull. Mus. Comp. Zool., **61**, p. 513.

Mops angolensis wonderi Sanborn, 1936, Field Mus. Nat. Hist., Zool. Ser., **20**, p. 114 (probably valid as a subspecies).

Mops osborni occidentalis Monard, 1939, Archos Mus. Bocage, **10**, p. 78.

Mops osborni fulva Monard, 1939, Archos Mus. Bocage, **10**, p. 78.

Mops angolensis orientis G. M. Allen and Loveridge, 1942, Bull. Mus. Comp. Zool., **79**, p. 166 (possibly valid as a subspecies).

Chaerephon emini: Wroughton, 1911, Ann. Mag. Nat. Hist., ser. 8, **8**, p. 458 (specimen from Rosieres [not *Nyctinomus emini* De Winton]).

Mops congica J. A. Allen

Mops congicus J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 467.

Mops demonstrator (Thomas)

Nyctinomus demonstrator Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, **12**, p. 504.

Mops (*Allomops*) *faradjius* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 476.

Chaerephon emini: G. M. Allen, 1914, Bull. Mus. Comp. Zool., **54**, p. 352 (specimen from Aradeiba [not *Nyctinomus emini* De Winton]).

Chaerephon bivittatus: G. M. Allen, 1914, Bull. Mus. Comp. Zool., **54**, p. 352 (specimens from El Garef [not *Nyctinomus bivittatus* Heuglin]).

Mops leonis (Thomas)

Nyctinomus leonis Thomas, 1908, Ann. Mag. Nat. Hist., ser. 8, **2**, p. 373.

Nyctinomus ochraceus J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 455 (possibly valid as a subspecies).

Mops midas (Sundevall)

Dysopes midas Sundevall, 1843, Kgl. Svenska Vetensk. Akad. Handl., p. 207.

Nyctinomus miarensis A. Grandidier, 1869, Rev. Mag. Zool., ser. 2, **21**, p. 337 (valid as a subspecies).

Nyctinomus unicolor A. Grandidier, 1870, Rev. Mag. Zool., ser. 2, **22**, p. 44.

Mops mops (de Blainville)

Dysopes mops F. Cuvier, 1824, Dents des Mamm., p. 250 (*nomen nudum*).

Molossus mops H. D. de Blainville, 1840, Osteogr. Vespertilio, p. 101.

Mops indicus Lesson, 1842, Nouv. Tabl. Regn. Anim., p. 18.

Mops nanula J. A. Allen

Mops (*Allomops*) *nanulus* J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 477.

Mops calabarensis Hayman, 1940, Trans. Zool. Soc. London, **24**, p. 677.

Mops niangarae J. A. Allen

Mops niangarae J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37**, p. 468.

Mops niveiventer Cabrera and Ruxton

Mops angolensis niveiventer Cabrera and Ruxton, 1926, Ann. Mag. Nat. Hist., ser. 9, **17,** p. 594.
Mops chitauensis Hill, 1937, Amer. Mus. Novitates, **916,** pp. 2, 3.

Mops sarasinorum (Meyer)

Nyctinomus sarasinorum Meyer, 1899, Abhandl. Zool. Anthrop.-Ethn. Mus. Dresden, ser. 7, **7,** p. 15, pls. 4, 10, 11.
Philippinopterus lanei Taylor, 1934, Philippine Land Mammals, p. 314 (Hill, 1961, listed it as a distinct species; I list it as a subspecies because it shows little difference from *M. sarasinorum* in a large preliminary study).

Mops spurrelli (Dollman)[10]

Xiphonycteris spurrelli Dollman, 1911, Ann. Mag. Nat. Hist., ser. 8, **7,** pp. 210, 211.

Mops thersites (Thomas)

Nyctinomus thersites Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, **12,** p. 634.
Mops (Allomops) occipitalis J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37,** p. 474.

Mops trevori J. A. Allen

Mops trevori J. A. Allen, 1917, Bull. Amer. Mus. Nat. Hist., **37,** p. 469.

Mormopterus Peters

Mormopterus Peters, 1865, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 258 (subgenus of *Nyctinomus*).
Mormopterus: Miller, 1907, Bull. U.S. Nat. Mus., **57,** p. 253 (listed only New World forms in the genus and included *M. norfolkensis* as a species of *Nyctinomus*).
Micronomus: Troughton, 1943, Furred animals of Australia, 2nd ed., p. 364 (listed earlier in Iredale & Troughton, 1934; includes only Australian forms).

Mormopterus (Mormopterus) acetabulosus (Hermann)

Vespertilio acetabulosus Hermann, 1804, Observationes Zoologicae, p. 19.
Dysopes natalensis A. Smith, 1847, Illustr. Zool. S. Africa, Mamm., pl. 49 and text (valid as a subspecies).
Mormopterus acetabulosus Miller, 1907, Bull. U.S. Nat. Mus., **57,** p. 254.

Mormopterus (Mormopterus) beccarii Peters

Mormopterus beccarii Peters, 1881, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 484.
Nyctinomus astrolabiensis Meyer, 1899, Abhandl. Zool. Anthrop.-Ethn. Mus. Dresden, ser. 7, **7,** p. 19 (valid as a subspecies).

---

[10]Probably an intensive study of males and females of both *M. spurrelli* and *M. nanula* should be done to see if these are actually one species.

Mormopterus (Mormopterus) doriae Andersen[11]

Mormopterus doriae Andersen, 1907, Ann. Mus. Civ. Stor. Nat. Genova, **3**, p. 38.

Mormopterus (Mormopterus) jugularis (Peters)

Nyctinomus (Mormopterus) jugularis Peters, 1865, in Sclater, Proc. Zool. Soc. London, **1865**, p. 468.
Nyctinomus albiventer Dobson, 1877, Proc. Zool. Soc. London, **1876**, p. 733.

Mormopterus (Mormopterus) kalinowskii (Thomas)

Nyctinomus kalinowskii Thomas, 1893, Proc. Zool. Soc. London, **1893**, p. 334.
Mormopterus kalinowskii: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 254.

Mormopterus (Mormopterus) loriae (Thomas)

Nyctinomus loriae Thomas, 1897, Ann. Mus. Civ. Stor. Nat. Genova, **18**, p. 609.
Tadarida loriae cobourgiana Johnson, 1959, Proc. Biol. Soc. Washington, **72**, p. 185.
Tadarida loriae ridei Felten, 1964, Senckenbergiana Biol., **45**, p. 6.

Mormopterus (Mormopterus) minutus (Miller)

Nyctinomus minutus Miller, 1899, Bull. Amer. Mus. Nat. Hist., **12**, p. 173.
Mormopterus minutus: Miller, 1907, Bull. U.S. Nat. Mus., **57**, p. 254.

Mormopterus (Mormopterus) norfolkensis (Gray)

Molossus norfolkensis Gray, 1839, Ann. Mag. Nat. Hist., ser. 11, **4**, p. 7.

Mormopterus (Mormopterus) phrudus (Handley)

Mormopterus phrudus Handley, 1956, Proc. Biol. Soc. Washington, **69**, p. 197.

Mormopterus (Mormopterus) planiceps (Peters)

Nyctinomus planiceps Peters, 1866, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 23.
Molossus wilcoxi Krefft, 1871, Austr. Vertebrata, fossil and recent, p. 4 (*nomen nudum*).
Nyctinomus petersi Leche, 1844, Proc. Zool. Soc. London, **1844**, p. 49.

Mormopterus (Platymops) setiger Peters

Mormopterus setiger Peters, 1878, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 196.
Platymops macmillani Thomas, 1906, Ann. Mag. Nat. Hist., ser. 7, **17**, p. 499 (valid as a subspecies).
Platymops barbatogularis Harrison, 1956, Ann. Mag. Nat. Hist., ser. 12, **9**, p. 549.
Platymops setiger: Harrison and Fleetwood, 1960, Durban Mus. Novitates, **15**, pp. 277–278.

Mormopterus (Sauromys) petrophilus (Roberts)

Platymops (Sauromys) petrophilus Roberts, 1917, Ann. Transvaal Mus., **6**, p. 4.

[11]Not included in my study.

Platymops (Sauromys) haagneri Roberts, 1917, Ann. Transvaal Mus., **5**, p. 5 (valid as a subspecies).

Platymops (Sauromys) haagneri umbratus Shortridge and Carter, 1938, Ann. S. African Mus., **32**, p. 282 (valid as a subspecies).

Platymops petrophilus erongensis Roberts, 1946, Ann. Transvaal Mus., **20**, p. 308.

Platymops petrophilus fitzsimonsi Roberts, 1946, Ann. Transvaal Mus., **20**, p. 308.

Sauromys petrophilus: Peterson, 1965, Life Sci. Contrib. Roy. Ontario Mus., **64**, p. 12.

Myopterus Geoffroy

Myopterus: Geoffroy, 1818, Description de l'Egypte, Paris, **2**, p. 113.

Eomops Thomas, 1905, Ann. Mag. Nat. Hist., ser. 7, **16**, p. 572.

Myopterus albatus Thomas

Myopterus senegalensis Oken, 1816, Lehrbuch der Naturg., **3**, p. 933 (original type specimen lost; name invalid).

Myopteris daubentonii Desmarest, 1820, Encyclopédie Méthodique Mammalogie, **1**, p. 132 (type specimen lost; Hill, 1969, suggested *incertae sedis;* Hayman & Hill, 1971, suspected synonymous with *albatus*).

Myopterus albatus Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, **16**, p. 469.

Myopterus whitleyi (Scharff)

Mormopterus whitleyi Scharff, 1900, Ann. Mag. Nat. Hist., ser. 7, **6**, p. 569.

Eomops whitleyi: Thomas, 1905, Ann. Mag. Nat. Hist., ser. 7, **16**, p. 572.

Nyctinomops Miller

Nyctinomops Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54**, p. 393.

Tadarida: Shamel, 1931, Proc. U.S. Nat. Mus., **78**, p. 1 (part, *macrotis* group).

Nyctinomops aurispinosa (Peale)

Dysopes aurispinosus Peale, 1848, U.S. Expl. Exp., 8, Mammalogy and Ornithology, p. 21 (Ed. 1).

Molossus aurispinosus: Cassin, 1858, U.S. Expl. Exp., 8, Mammalogy and Ornithology, pp. 5–7 (Ed. 2).

Nyctinomops aurispinosus: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54**, p. 393.

Tadarida aurispinosa: Shamel, 1931, Proc. U.S. Nat. Mus., **78**, p. 11.

Tadarida similis Sanborn, 1941, Field Mus. Nat. Hist., Zool. Ser., **27**, p. 386.

Nyctinomops femorosacca (Merriam)

Nyctinomus femorosaccus Merriam, 1889, N. Amer. Fauna, no. 2, p. 23.

Nyctinomops femorosaccus: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54**, p. 393.

Tadarida femorosacca: Miller, 1924, Bull. U.S. Nat. Mus., **128**, p. 86.

Nyctinomops laticaudata (Geoffroy)

Molossus laticaudatus Geoffroy, 1805, Ann. Mus. Paris, **6**, p. 156.

Molossus caecus Rengger, 1830, Säugethiere Paraguay, p. 88.

Nyctinomus gracilis Dobson, 1876, Proc. Zool. Soc. London, **1876,** p. 731.

Nyctinomus europs H. Allen, 1889, Proc. Amer. Philos. Soc., **26,** pp. 558–561.

Nyctinomops yucatanicus Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54,** p. 393 (valid as a subspecies).

Nyctinomops laticaudata: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54,** p. 393.

Tadarida laticaudata: Shamel, 1931, Proc. U.S. Nat. Mus., **78,** p. 12.

Tadarida laticaudata ferruginea Goodwin, 1954, Amer. Mus. Novitates, 1607, p. 2.

Tadarida laticaudata macarenensis Barriga-Bonilla, 1965, Caldasia (Colombia), **9,** p. 249.

Nyctinomops macrotis (Gray)

V(espertilio) Molossus (part) Pallas, 1766, Miscellanea Zoologica, pp. 49–50.

Nyctinomus macrotis Gray, 1839, Ann. Mag. Nat. Hist., ser. 11, 4, p. 5.

Dysopes auritus Wagner, 1843, Arch. Naturg., **9,** pt. 1, p. 368.

Nyctinomus megalotis Dobson, 1876, Proc. Zool. Soc. London, **1876,** p. 728.

Nyctinomus depressus Ward, 1891, Amer. Nat., **23,** p. 747.

Promops affinis J. A. Allen, 1900, Bull. Amer. Mus. Nat. Hist., **13,** p. 91.

Promops depressus: J. A. Allen, 1900, Bull. Amer. Mus. Nat. Hist., **13,** p. 91.

Nyctinomops macrotis: Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, **54,** p. 393.

Nyctinomus nevadensis Miller, 1902, Proc. Biol. Soc. Washington, **15,** p. 250.

Nyctinomus molossus: Miller, 1913, Proc. U.S. Nat. Mus., **46,** p. 86 (footnote 4).

Nyctinomus aequatorialis J. A. Allen, 1914, Bull. Amer. Mus. Nat. Hist., **33,** p. 386.

Tadarida molossa: Hershkovitz, 1949, Proc. U.S. Nat. Mus., **99,** p. 452.

Tadarida macrotis: Husson, 1962, The bats of the Suriname, E. J. Brill, Leiden, pp. 256–259.

Otomops Thomas

Otomops Thomas, 1913, J. Bombay Nat. Hist. Soc., **22,** p. 90.

Otomops formosus Chasen[12]

Otomops formosus Chasen, 1939, Treubia, **17,** p. 186.

Otomops martiensseni (Matschie)

Nyctinomus martiensseni Matschie, 1897, Arch. Naturg., **63,** pt. 1, p. 84.

Otomops icarus Chubb, 1917, Ann. Durban Mus., **1,** p. 433 (valid as a sub-species).

Otomops madagascarensis Dorst, 1953, Mem. Inst. Sci. Madagascar, ser. A, 8, p. 236 (valid as a subspecies; Valdivieso et al., 1979, listed it as a distinct species).

Otomops papuensis Lawrence

Otomops papuensis Lawrence, 1948, J. Mamm., **29,** p. 413.

[12]Not included in my study.

Otomops secundus Hayman

Otomops secundus Hayman, 1952, Bull. Brit. Mus. (Nat. Hist.), Zool., **1,** p. 314.

Otomops wroughtoni

Otomops wroughtoni Thomas, 1913, J. Bombay Nat. Hist. Soc., **22,** p. 91.

Philippinopterus see *Mops*

Platymops see *Mormopterus*

Promops Gervais

Promops Gervais, 1855, Mammiferes, *in* Castelnau, Exped. dans les partes centrales de l'Amer. du Sud. . . . pt. 7, p. 58. (Type *Promops ursinus* Gervais = *Molossus nasutus* Spix.)

Promops centralis Thomas

Promops centralis Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, **16,** p. 62.
Promops occultus Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, **16,** p. 62 (valid as a subspecies).
Promops davisoni Thomas, 1921, Ann. Mag. Nat. Hist., ser. 8, **8,** p. 139 (valid as a subspecies).[13]

Promops nasutus (Spix)

Molossus nasutus Spix, 1823, Sim. Vespert. Brasil., p. 59.
Molossus fumarius Spix, 1823, Sim. Vespert. Brasil., p. 60.
Dysopes rufocastaneus Schinz, 1844, Syst. Verz. Säug., **1,** 142.
Promops ursinus Gervais, 1855, Mammiferes, *in* Castelnau, Exped. dans les partes centrales de l'Amer. du Sud. . . . pt. 7, p. 59.
Promops fosteri Miller, 1907, Bull. U.S. Nat. Mus., **57,** p. 259.
Promops nasutus: Miller, 1907, Bull. U.S. Nat. Mus., **57,** p. 260.
Promops pamana Miller, 1913, Proc. Biol. Soc. Washington, **26,** p. 33.
Promops ancilla Thomas, 1915, Ann. Mag. Nat. Hist., ser. 8, **16,** p. 63 (valid as a subspecies).
Promops nasutus downsi Goodwin, 1962, Amer. Mus. Novitates, **2080,** p. 10 (possibly valid as a subspecies).

Sauromys see *Mormopterus*

Tadarida Rafinesque

Tadarida Rafinesque, 1814, Précis des découvertes et travaux somiologiques. . . . , p. 55 (Type, *Cephalotes teniotes* Rafinesque).
Nyctinomus E. Geoffroy, 1818, Description de l'Egypte, **2,** p. 114 (Type, *Nyctinomus aegyptiacus* E. Geoffroy).

---

[13]Ojasti & Linares (1971) thought that *P. davisoni* was a subspecies of *P. centralis.* Koopman (1978) agreed, but did not mention comparing *davisoni* with *nasutus.* Specimens of *davisoni* from AMNH which I measured were more similar to *nasutus* than to *centralis* in my large preliminary study, which is why I list *davisoni* with *nasutus* in specimens examined. Both are of similar small size, with *centralis* being the larger.

Nyctinoma Bowdich, 1821, Anal. Nat. Class. Mamm., p. 288.

Nyctinomes Gray, 1821, London Med. Repos., **15**, p. 299.

Nyctinomia Fleming, 1822, Philos. Zool., **2**, p. 178.

Dinops Savi, 1825, N. Gior. Lett. Pisa, Sci., **10**, p. 229 (*Dinops cestoni* Savi = *Cephalotes teniotis* Rafinesque).

Dysopes: Cretzschmar, 1830 or 1831, *in* Ruppell, Atlas zu der Reise im nordlichen Afrika, Säugethiere, p. 69 (not of Illiger, 1811).

Austronomus Iredale and Troughton, 1934, Mem. Austral. Mus., **6**, p. 100 (*nomen nudam;* later validated by Troughton, 1941, Furred animals of Australia, ed. 1, p. 360).

Tadarida aegyptiaca (E. Geoffroy)

Nyctinomus aegyptiacus E. Geoffroy, 1818, Description de l'Egypte, **2**, p. 128, pl. 2, no. 2.

Dysopes geoffroyi Temmink, 1827, Monogr. Mammal., **1**, p. 226.

Nyctinomus tragatus Dobson, 1874, J. Asiatic Soc. Bengal, **43**, ser. 2, p. 143.

Dysopes talpinus Heuglin, 1877, Reise in Nordost-Afrika. Braunschweig, vol. 2, p. 28.

Nyctinomus anchietae Seabra, 1900, J. Sci. Math. Phys. Nat., Lisboa, **6**, p. 82.

Nyctinomus brunneus Seabra, 1900, J. Sci. Math. Phys. Nat., Lisboa, **6**, p. 83.

Nyctinomus bocagei Seabra, 1900, J. Sci. Math. Phys. Nat., Lisboa, **6**, p. 84 (valid as a subspecies).

Nyctinomus tongaensis Wettstein, 1916, Anz. K. Akad. Wiss. Wien, **53**, p. 192.

Tadarida sindica Wroughton, 1919, J. Bombay Nat. Hist. Soc., **26**, p. 732 (valid as a subspecies).

Tadarida thomasi Wroughton, 1919, J. Bombay Nat. Hist. Soc., **26**, p. 732 (valid as a subspecies).

Tadarida gossei Wroughton, 1919, J. Bombay Nat. Hist. Soc., **26**, pp. 732–733 (valid as a subspecies).

Tadarida africana (Dobson)[14]

Nyctinomus africanus Dobson, 1876, Ann. Mag. Nat. Hist., ser. 4, **17**, p. 348.

Tadarida australis (Gray)

Molossus australis Gray, 1838, Mag. Zool. Bot., **2**, p. 501.

Nyctinomus albidus Leche, 1884, Proc. Zool. Soc. London, **1884**, p. 58, fig. 3.

Nyctinomus australis atratus Thomas, 1924, Ann. Mag. Nat. Hist., ser. 9, **14**, p. 456.

Austronomus australis: Troughton, 1941, Furred Animals of Australia, ed. 1, p. 360.

Tadarida brasiliensis (I. Geof. St.-Hilaire)

Nyctinomus brasiliensis I. Geoffroy St.-Hilaire, 1824, Ann. Sci. Nat., **1**, p. 343.

Dysopes nasutus Temminck, 1827, Monogr. Mammal., **1**, p. 233.

---

[14]According to Dieter Kock (1975, Stuttgarter Beiträge zur Naturkunde, ser. A. (Biol.), no. 272, pp. 1–9), the earliest name for *africana* was *Nyctinomus (Dysopes) ventralis* Heuglin, 1861, Nov. Act. Acad. Caes. Leop.-Carol., **29**, pp. 4, 11. This name came to my attention only recently.

Nyctinomus murinus Gray, 1827, Cuvier's Animal Kingdom, Griffith ed., **5**, p. 66 (valid as a subspecies).

Nyct(icea) cynocephala LeConte, 1831, Cuvier's Animal Kingdom, McMurtie's edition, **1**, p. 432 (valid as a subspecies).

Molossus fulginosus Cooper, 1837, Ann. Lyc. Nat. Hist. New York, **4**, p. 67.

Dysopes naso Wagner, 1840, *in* Schreber, Die Säugethiere, Suppl., **1**, p. 475.

Rhinopoma carolinensis Gundlach (not Geoffroy), 1840, Wiegm. Archiv., **1**, p. 358.

Molossus mexicanus Saussure, 1860, Rev. Mag. Zool., Paris, ser. 2, **12**, p. 283 (valid as a subspecies).

Nyctinomus musculus Gundlach, 1861, Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 149 (valid as a subspecies).

Nyctinomus mohavensis Merriam, 1889, N. Amer. Fauna, no. 2, p. 25.

Nyctinomus antillularum Miller, 1902, Proc. Acad. Nat. Sci. Philadelphia, p. 398 (valid as a subspecies).

Nyctinomus bahamensis Rehn, 1902, Proc. Acad. Nat. Sci. Philadelphia, p. 641 (valid as a subspecies).

Mormopterus peruanus J. A. Allen, 1914, Bull. Amer. Mus. Nat. Hist., **33**, p. 311.

Tadarida intermedia Shamel, 1931, Proc. U.S. Nat. Mus., **78**, p. 7 (valid as a subspecies).

Tadarida constanzae Shamel, 1931, Proc. U.S. Nat. Mus., **78**, p. 10 (valid as a subspecies).

Tadarida texana Stager, 1942, Bull. Southern California Acad. Sci., **41**, p. 49.

Tadarida espiritosantensis (Ruschi)[15]

Tadarida espiritosantensis Ruschi, 1951, Bol. Mus. Biol. Prof. Mello-Leitão Zool., Santa Teresa, Espírito Santo, no. 7, p. 19.

Tadarida fulminans (Thomas)

Nyctinomus fulminans Thomas, 1903, Ann. Mag. Nat. Hist., ser. 7, **12**, p. 501.

Tadarida mastersoni Roberts, 1946, Ann. Transvaal Mus., **20**, p. 306.

Tadarida kuboriensis McKean and Calaby[16]

Tadarida kuboriensis McKean and Calaby, 1968, Mammalia, **32**, p. 375.

Tadarida lobata (Thomas)

Nyctinomus lobatus Thomas, 1891, Ann. Mag. Nat. Hist., ser. 6, **7**, p. 303.

Tadarida teniotis (Rafinesque)

Cephalotes teniotis Rafinesque, 1814, Précis. Découv. Somiol., p. 12.

Dinops cestoni Savi, 1825, N. Giorn. Lett. Pisa, Sci., **10**, p. 235.

Dysopes rupelii (sic) Temminck, 1826, Monogr. Mammal., **1**, p. 224, pl. 18 (valid as a subspecies).

Dysopes savii Schinz, 1840, European Fauna, **1**, p. 5.

Nyctinomus insignis Blyth, 1861, J. Asiatic Soc. Bengal, **30**, p. 90 (valid as a subspecies).

---

[15]Mentioned in Pine & Ruschi, 1976, An. Inst. Biol. Univ. Autón. Mexico, **47**, ser. Zool., pp. 183–196; not included in my study.

[16]This may eventually prove to be a subspecies of *T. australis*.

Nyctinomus taeniotis Thomas, 1891, Proc. Zool. Soc. London, **1891,** p. 182.

Dysopes midas: Schulze, 1897, Helios, Berlin, **14,** p. 95 (not of Sundevall, 1842).

Tadarida latouchei Thomas, 1920, Ann. Mag. Nat. Hist., ser. 9, **5,** p. 283.

Tadarida septentrionalis Kishida and Mori, 1931, Zool. Mag. Tokyo, **43,** p. 379
    (*nomen nudum*).

Vespertilio see *Eumops*

Xiphonycteris see *Mops*

APPENDIX C

KEY TO GENERA AND SUBGENERA OF MOLOSSID BATS

1a. Ears usually widely separated, basisphenoid pits usually shallow or
    nonexistent (*Myopterus* an exception).
  2a. Palate without anterior emargination, no wrinkles on lips.
    3a. Tooth number 26 (1/1, 1/1, 1/2, 3/3), M³ V-shaped, 2nd phalanx of
        digit IV from 16–20 per cent of total length of digit IV.
      4a. Body size very large (FA around 75 mm, GSL near 30 mm),
          hair short and sparse to the point of being naked . . . .
                                                        Cheiromeles
      4b. Body size smaller.
        5a. Basisphenoid pits very deep (distinct hole 1+mm in
            depth) . . . .*Myopterus*
        5b. Basisphenoid pits shallow, slight cusp on M³, size
            very small(GSL near 13 mm). . .*Molossops (Molossops)*
    3b. Tooth number 28 or 30, M³ either V- or N-shaped, 2nd phalanx
        variable.
      6a. Tooth formula 1/2(1), 1/1, 1/2, 3/3 = 28 (26 possibly), 2nd
          phalanx of digit IV near 7.5 per cent (6.9–8.5) of digit IV, M³
          V-shaped . . . .*Molossops (Cynomops)*
      6b. Tooth formula 1/2, 1/1, 2/2, 3/3 = 30, 2nd phalanx of digit IV
          near 12 per cent of digit IV, M³ N-shaped . . . .
                                          Molossops (Neoplatymops)
  2b. Palate notched anteriorly, coronoid process usually high and curved
      posteriorly, lips not wrinkled or slightly wrinkled or covered with
      spines.
    7a. Skull not extremely flattened, 28–30 teeth, M³ complete N-shape.
      8a. Tooth formula 1/2, 1/1, 1/2, 3/3 . . .New World *Mormopterus*
      8b. Tooth formula 1/3, 1/1, 1/2, 3/3 or 1/2, 1/1, 2/2, 3/3 . . . .
                                          Old World *Mormopterus*
    7b. Skull extremely flattened.
      9a. PM³ absent, extreme development of lacrimal process, lips
          covered with thick, spiny hairs . .*Mormopterus (Platymops)*
      9b. PM³ present (ears not widely separated but meeting in a
          V) . . . .*Mormopterus (Sauromys)*
1b. Ears not widely separated but just joining to form a V-shaped valley or
    well-joined over the nose by a band; basisphenoid pits usually medium
    deep to very deep.

10a. No anterior emargination of palate.
    11a. Lips unwrinkled, M^3 V-shaped.
        12a. PM^3 absent ....*Molossus*
        12b. PM^3 vestigial, domed-palate ....*Promops*
    11b. Lips skirt-like with many fine wrinkles, PM^3 present, ears often large and forward facing, M^3 variable but usually always with posterior commissure ....*Eumops*
10b. Anterior emargination of palate either slight or deep, lips either deeply wrinkled or skirt-like.
    12a. 2nd phalanx of digit IV 9 per cent or greater of digit IV length.
        13a. M^3 V-shaped or with slight posterior cusp (less than half of length of 2nd cusp), PM^3 moderately developed, vestigial or absent, dentary relatively thick (lateral thickness at M_1 11–15 per cent of dentary length), 4 or 2 lower incisors ....
                                  Mops
        13b. M^3 not always fully developed N-shape but posterior cusp greater than half of length of 2nd cusp, palatal emargination usually slight, relative thickness of dentary rarely over 11 per cent (*Chaerephon jobensis* from Indo-Australian region an exception with about 14 per cent), 2nd phalanx of digit IV around 14–17 per cent ....*Chaerephon*
        13c. M^3 usually well-developed N-shape, deeply notched anterior palate, PM^3 usually well developed, 2nd phalanx of digit IV usually 9–12 per cent of digit IV (the Australian *Tadarida australis* and New Guinean *T. kuboriensis* are exceptions at 17 per cent of digit IV) ....*Tadarida*
        14. If basisphenoid extremely deep ....*Otomops*
        15. If skull extremely flattened ...*Mormopterus (Sauromys)*
    12b. 2nd phalanx between 3 and 5 per cent of digit IV, narrow rostrum and deeply notched anterior palate ....*Nyctinomops*

LITERATURE CITED

AELLEN, V. 1970. Le baculum de *Tadarida teniotis*. Bijd. Dierk., **40**:8–9.

ALLEN, G. M. 1939. Bats. New York, Dover Publications, Inc., x + 368 pp.

ALLEN, J. A., HERBERT LANG, AND JAMES P. CHAPIN. 1917. The American Museum Congo Expedition collection of bats. Part I. Systematic list (Allen); Part II. Notes on the distribution and ecology of central African Chiroptera (Lang & Chapin); Part III. Field notes (Lang & Chapin). Bull. Amer. Mus. Nat. Hist., **37**:405–563, pls. 44–55, 26 figs., map.

ALLISON, VERNON C. 1937. Evening bat flight from Carlsbad Caverns. J. Mammal., **18**:80–82.

BAILEY, VERNON. 1931. Mammals of New Mexico. North Amer. Fauna, no. 53, pp. 1–412, pls. 1–22.

BLACK, HAL L. 1974. A north temperate bat community: Structure and prey populations. J. Mammal., **55**:138–157.

BROSSET, ANDRÉ. 1963. The bats of Central and Western India. J. Bombay Nat. Hist. Soc., **60**:337–355.

————. 1966. La Biologie des Chiroptères. Paris, Masson et Cie, Editeurs, vii + 240 pp.

BROSSET, ANDRÉ, AND G. DUBOST. 1967. Chiroptères de la Guyana Française. Mammalia, **31**:583–594.

Brown, Randall E. 1967. Bacula of some New World molossid bats. Mammalia, 31:643–667.

Carter, Dilford C., and William B. Davis. 1961. *Tadarida aurispinosa* (Peale) (Chiroptera: Molossidae) in North America. Proc. Biol. Soc. Washington, 74:161–166.

Carter, Dilford C., Ronald H. Pine, and William B. Davis. 1966. Notes on Middle American bats. Southwestern Nat., 11:488–499.

Crompton, A. W., and Karen Hiiemäe. 1969. How mammalian molar teeth work. Discovery, 5:23–34.

Dulic, Beatrica, and Festo A. Mutere. 1973. Comparative study of the chromosomes of some molossid bats from eastern Africa. Periodicum Biologorum, 75:61–65.

Dwyer, P. D. 1965. Flight patterns of some eastern Australian bats. Victorian Nat., 82:36–41.

Easterla, David A., and John O. Whitaker. 1972. Food habits of some bats from Big Bend National Park, Texas. J. Mammal., 53:887–890.

Eger, Judith L. 1977. Systematics of the genus *Eumops* (Chiroptera: Molossidae). Life Sci. Contrib., Roy. Ontario Mus., 110:1–69.

Ellerman, J. R., and T. C. S. Morrison-Scott. 1951. Checklist of Palearctic and Indian Mammals. 1758 to 1946. London, British Museum (Natural History), 810 pp.

Fearnhead, R. W., C. C. D. Shute, and A. d'A. Bellairs. 1955. The temporo-mandibular joint in shrews. Proc. Zool. Soc. London, 125:795–806 + plate.

Fenton, M. Brock. 1972. The structure of aerial-feeding bat faunas as indicated by ears and wing elements. Canadian J. Zool., 50: 287–296.

———. 1975. Acuity of echolocation in *Collocalia hirundinacea* (Aves: Apodidae), with comments on the distributions of echolocating swiftlets and molossid bats. Biotropica, 7:1–7.

Fenton, M. Brock, and Theodore H. Fleming. 1976. Ecological interactions between bats and nocturnal birds. Biotropica, 8:104–110.

Fenton, M. Brock, and Randolph L. Peterson. 1972. Further notes on *Tadarida aloysiisabaudiae* and *Tadarida russata* (Chiroptera: Molossidae-Africa). Canadian J. Zool., 50:19–24.

Findley, James S. 1972. Phenetic relationships among bats of the genus *Myotis*. Syst. Zool., 21:31–52.

———. 1973. Phenetic packing as a measure of faunal diversity. Amer. Nat., 107:580–584.

———. 1975. The structure of bat communities. Amer. Nat., 110:129–139.

Findley, James S., Eugene H. Studier, and Don E. Wilson. 1972. Morphologic properties of bat wings. J. Mammal., 53:429–444.

Gardner, A. L. 1977. Taxonomic implications of the karyotypes of *Molossops* and *Cynomops* (Mammalia: Chiroptera). Proc. Biol. Soc. Washington, 89:545–550.

Glass, Bryan P. 1953. Variation in the lower incisors of the Mexican free-tailed bat, *Tadarida mexicana* (Saussure). Proc. Oklahoma Acad. Sci., 34:73–74.

Goodwin, George G. 1940. Three new bats from Honduras and the first record of *Ethisthenes harti* (Thomas) for North America. Amer. Mus. Novitates, 1075:1–3.

———. 1958. Three new bats from Trinidad. Amer. Mus. Novitates, 1877:1–6.

———. 1959. Descriptions of some new mammals. Amer. Mus. Novitates, 1967:1–8.

Hall, E. Raymond, and Keith R. Kelson. 1959. The mammals of North America. New York, The Ronald Press Co., 2 vols., xxx + 1083 pp.

Hall, Leslie S., and G. C. Richards. 1972. Notes on *Tadarida australis* (Chiroptera: Molossidae). Australian Mammal., 1:46–47.

Handley, Charles O., Jr. 1956. A new species of free-tailed bat (genus *Mormopterus*) from Peru. Proc. Biol. Soc. Washington, 69:197–202.

———. 1966. Checklist of mammals, pp. 753–793. *In* Wenzel, R. L., and V. J. Tipton (eds.), Ectoparasites of Panama. Chicago, Field Mus. Nat. Hist., xiii + 861 pp.

Harrison, David L. 1962. On bats collected on the Limpopo River, with the description of a new race of the tomb bat, *Taphozous sudani* Thomas, 1915. I. Systematic notes. Occas. Pap. Natl. Mus. S. Rhodesia, 26B: 755–767, 4 pls.

————. 1971. A note on the occurrence of the giant African free-tailed bat, *Tadarida africana* (Dobson, 1876), in Tanzania, with some observations on the characters of the species. Arnoldia, Nat. Mus. Rhodesia, **5**:1–5.

HARRISON, J. L. 1954. The wing pouches of the naked bulldog bat. Malayan Nat. J., **9**:66–67.

HARRISON, T., AND LORD MEDWAY. 1959. 'Bat erosion' at Niah Great Caves. Nature, **183**:931.

HARTMAN, FRANK A. 1963. Some flight mechanisms of bats. Ohio J. Sci., **63**:59–63.

HAYMAN, R. W., AND J. E. HILL. 1971. The mammals of Africa. An identification manual. Part 2. Order Chiroptera. Washington, D.C., Smithsonian Institution Press, 173 pp.

HAYWARD, BRUCE J., AND RUSSELL DAVIS. 1964. Flight speeds in western bats. J. Mammal., **45**:236–242.

HERRING, SUSAN W., AND STEPHEN E. HERRING. 1974. The superficial masseter and gape in mammals. Amer. Nat., **108**:561–576.

HILDEBRAND, MILTON. 1974. Analysis of vertebrate structure. New York, John Wiley and Sons. xv + 710 pp.

HILL, J. E. 1961. Indo-Australian bats of the genus *Tadarida*. Mammalia, **25**:29–56.

————. 1969. The status of *Myopterus senegalensis* Oken, 1816 (Chiroptera: Molossidae). Mammalia, **33**:727–729.

HOWELL, D. J., AND DEREK BURCH. 1974. Food habits of some Costa Rican bats. Rev. Biol. Trop., **21**:281–294.

HUSSON, ANTONIUS MARIE. 1962. The bats of the Suriname. Leiden, E. J. Brill, 1–282 pp., 1–30 plates.

IRWIN, MICHAEL P. S., AND B. DONNELLY. 1962. On bats collected on the Limpopo River. . . . II. A general description of the area with notes on habitat and ecology. Occas. Pap. Nat. Mus. S. Rhodesia, **26B**:767–769.

JOHNSON, DAVID H. 1959. Four new mammals from the Northern Territory of Australia. Proc. Biol. Soc. Washington, **72**:183–188.

JONES, J. KNOX, JR. 1966. Bats from Guatemala. Univ. Kansas Publ., Mus. Nat. Hist., **16**:439–472.

JONES, J. KNOX, JR., AND PATRICK B. DUNNIGAN. 1965. *Molossops greenhalli* and other bats from Guerrero and Oaxaca, Mexico. Trans. Kansas Acad. Sci., **68**:461–462.

JONES, J. KNOX, JR., AND HUGH H. GENOWAYS. 1967. A new subspecies of the free-tailed bats, *Molossops greenhalli*, from western Mexico (Mammalia; Chiroptera). Proc. Biol. Soc. Washington, **80**:207–210.

JONES, J. KNOX, JR., JAMES DALE SMITH, AND RONALD W. TURNER. 1971. Noteworthy records of bats from Nicaragua, with a checklist of the chiropteran fauna of the country. Occas. Pap. Mus. Nat. Hist. Univ. Kansas, **2**:1–35.

KALLEN, FRANK C., AND CARL GANS. 1972. Mastication in the little brown bat *Myotis lucifugus*. J. Morphol., **136**:385–420.

KINGDON, JONATHAN. 1974. East African mammals. An atlas of evolution in Africa. Vol. II part A (insectivores and bats). London and New York, Academic Press, xi + 341 + A1 pp.

KITCHENER, H. J. 1954a. A naked bulldog bat. Malayan Nat. J., **8**:165–166 + plate.

————. 1954b. A further note on the naked bulldog bat. Malayan Nat. J., **9**:26–28.

KOCK, DIETER. 1969. Über ein weibliches Exemplar der afrikanischen Bulldogg-Fledermäus, *Xiphonycteris spurrelli*, von Fernando Poo (Mammalia, Chiroptera). Senckenbergiana biol., **50**:9–13.

————. 1973. Merkmalsdifferenzen tropischer Fledermäuse. Z. Säuge., **38**:129–143.

KOOPMAN, KARL F. 1965. Status of forms described or recorded by J. A. Allen in "The American Museum Congo Expedition collection of bats." Amer. Mus. Novitates, **2219**:1–34.

————. 1968. Taxonomic and distributional notes on Lesser Antillean bats. Amer. Mus. Novitates, **2333**:1–13.

————. 1970. Zoogeography of bats, pp. 29–50. *In* Slaughter, B. H., and D. W. Walton (eds.), About bats. Dallas, Southern Methodist Univ. Press, vii + 339 pp.

————. 1975. Bats of the Sudan. Bull. Amer. Mus. Nat. Hist., **154**:353–444.

————. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. Amer. Mus. Novitates, **2651**:1–33.

KRUTZSCH, P. H. 1944. Notes on the little known pocketed bat. J. Mammal., **25**:201.

————. 1955. Observations on the California mastiff bat. J. Mammal., **36**:407–414.

LANG, HERBERT, AND JAMES P. CHAPIN. 1917. *See* Allen, J. A., Herbert Lang, and James P. Chapin.

LAVAL, RICHARD K. 1969. Records of bats from Honduras and El Salvador. J. Mammal., **50**:819–822.

LAWLOR, TIMOTHY E. 1973. Aerodynamic characteristics of some Neotropical bats. J. Mammal., **54**:71–78.

MAGLIO, V. J. 1973. Origin and evolution of the Elephantidae. Trans. Amer. Philos. Soc., **63**, pt. 3:1–149.

MARINKELLE, C. J. 1970. Redescription of *Eumops bonariensis delticus* Thomas, 1923 (Chiroptera, Molossidae). Rev. Brasil. Biol., Rio de Janeiro, **30**:461–464.

MAYNARD SMITH, J., AND R. J. G. SAVAGE. 1959. The mechanics of mammalian jaws. School Sci. Rev., **40**(141):289–301.

MCKEAN, JOHN L., AND JOHN H. CALABY. 1968. A new genus and two new species of bats from New Guinea. Mammalia, **32**:372–378.

MCKEAN, JOHN L., AND ELERY HAMILTON-SMITH. 1967. Litter size and maternity sites of Australian bats (Chiroptera). Victorian Nat., **84**:203–206.

MCKEAN, J. L., AND W. J. PRICE. 1967. Notes on Chiroptera from Queensland, Australia. Mammalia, **31**:101–119.

MCNAB, BRIAN K. 1971. The structure of tropical bat faunas. Ecology, **52**:352–358.

MEDWAY, LORD. 1958. 300,000 bats. Sarawak Mus. J., 8:667–679.

MILLER, GERRIT S. 1902. Twenty new American bats. Proc. Acad. Nat. Sci. Philadelphia, **54**:389–412.

————. 1907. The families and genera of bats. Bull. U.S. Nat. Mus., **57**:i–282.

————. 1913. Notes on the genus Molossus. Proc. U.S. Nat. Mus., **46**:85–92.

MILLER, G. S., AND N. HOLLISTER. 1921. Twenty new mammals collected by H. C. Raven in Celebes. Proc. Biol. Soc. Washington, **34**:93–104.

MUTERE, FESTO A. 1973. A comparative study of reproduction in two populations of the insectivorous bat, *Otomops martiensseni*, at latitudes 1°5'S and 2°30'S. J. Zool., London, **171**:79–92.

OJASTI, JUHANI, AND OMAR J. LINARES. 1971. Adiciones a la fauna de murcielagos de Venezuela con notas sobre las especies del genero *Diclidurus* (Chiroptera). Acta Biol. Venez., **7**:421–441.

PETERS, W. 1878. Über die von Hon. J. J. Hildebrant während seiner letzten ostrafrikanischen Reise gesammelten Säugthiere und Amphibien. Monatsber. K. Preuss. Akad. Wiss. Berlin, pp. 194–209.

PETERSON, RANDOLPH L. 1965. A review of the flat-headed bats of the family Molossidae from South America and Africa. Life Sci. Contrib., Roy. Ontario Mus., **65**:1–32.

————. 1967. A new record for the African molossid bat *Tadarida aloysiisabaudiae*. Canadian J. Zool., **45**:449–452.

————. 1969. Further notes on the African molossid bat *Tadarida aloysiisabaudiae*. Los Angeles County Mus. Contrib. Sci., **161**:1–6.

————. 1971a. The African molossid bat *Tadarida russata*. Canadian J. Zool., **49**:297–301.

————. 1971b. The systematics of the African molossid bats *Tadarida bemmelini* and *Tadarida cistura*. Canadian J. Zool., **49**:1347–1354.

————. 1972. Systematic status of the African molossid bats *Tadarida congica, T. niangarae,* and *T. trevori*. Life Sci. Contrib., Roy. Ontario Mus., **85**:1–32.

——. 1974. Variation in the African bat, *Tadarida lobata*, with notes on habitat and habits (Chiroptera: Molossidae). Life Sci. Occas. Pap., Roy. Ontario Mus., **24**:1–8.

PETERSON, RANDOLPH L., AND DAVID L. HARRISON. 1970. The second and third known specimens of the African molossid bat, *Tadarida lobata*. Life Sci. Occas. Pap., Roy. Ontario Mus., **16**:1–6.

PINE, RONALD H. 1969. Stomach contents of a free-tailed bat, *Molossus ater*. J. Mammal., **50**:162.

PYE, ADE. 1966. The structure of the cochlea in Chiroptera II. The Megachiroptera and Vespertilionoidea of the Microchiroptera. J. Morphol., **119**:101–120.

ROER, HUBERT. 1971. Zur Lebensweise einiger Microchiropteren der Namibwüste (Mammalia, Chiroptera). Zool. Abhandl. Staatl. Mus. Tierk. Dresden, **32**:43–55.

ROHLF, F. JAMES, JOHN KISHPAUGH, AND DAVID KIRK. 1974. Numerical taxonomy system of multivariate statistical programs (NT-SYS). The State University of New York at Stony Brook.

ROSEVEAR, D. R. 1965. The bats of West Africa. British Mus. (Nat. Hist.), ixvii + 418 pp.

ROSS, ANTHONY. 1967. Ecological aspects of the food habits of insectivorous bats. Proc. West. Found. Vert. Zool., **1**:205–264, 15 figs.

SANBORN, COLIN C. 1932. The bats of the genus *Eumops*. J. Mammal., **13**:348–357.

——. 1953. The Cuban free-tailed bat, *Mormopterus minutus* Miller. J. Mammal., **34**:383.

SAZIMA, IVAN, AND VALDIR A. TADDEI. 1976. A second Brasilian record of the South American flat-headed bat, *Neoplatymops mattogrossensis*. J. Mammal., **57**:757–758.

SCHNELL, GARY D. 1970. A phenetic study of the suborder Lari (Aves) I. Methods and results of principal components analyses; II. Phenograms, discussion, and conclusions. Syst. Zool., **19**:35–57, 264–302 (2 parts).

SCHOENER, THOMAS W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution, **19**:189–213.

——. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology, **49**:704–726.

SCHUM, G. MICHAEL. 1972. The use of low frequency sounds for echoranging by *Tadarida macrotis*. Unpublished Masters Thesis, University of New Mexico, 34 pp.

SHAMEL, H. HAROLD. 1931. Notes on the American bats of the genus *Tadarida*. Proc. U.S. Nat. Mus., **78**:1–27.

SHERMAN, H. B. 1939. Notes on the food of some Florida bats. J. Mammal., **20**:103–104.

SHORTRIDGE, G. C. 1936. Field notes of Western Australian mammals. . . . Proc. Zool. Soc. London, **1936**:743–749.

SILVA-TOBOADA, GILBERTO, AND KARL F. KOOPMAN. 1964. Notes on the occurrence and ecology of *Tadarida laticaudata yucatanica* in eastern Cuba. Amer. Mus. Novitates, **2175**:1–6.

SIMMONS, J. A., W. A. LAVENDER, B. A. LAVENDER, J. E. CHILDS, H. KULEBAK, M. R. RIGDEN, J. SHERMAN, B. WOOLMAN, AND M. J. O'FARRELL. 1978. Echolocation in free-tailed bats (*Tadarida*). J. Comp. Physiol., A, **125**:291–300.

SIMPSON, GEORGE G. 1944. Tempo and mode in evolution. New York, Columbia Univ. Press, xviii + 237 pp.

——. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85**, xvi+350 pp.

SIMPSON, GEORGE G., ANNE ROE, AND RICHARD C. LEWONTIN. 1960. Quantitative zoology. Revised edition. New York, Chicago, San Francisco, Atlanta; Harcourt, Brace and World, Inc., vii + 440 pp.

SLAUGHTER, BOB H. 1970. Evolutionary trends of chiropteran dentition, pp. 51–83. *In* Slaughter, B. H., and D. W. Walton (eds.), About bats. Dallas, Southern Methodist Univ. Press, vii + 339 pp.

SMITH, JAMES D. 1976. Chiropteran evolution, pp. 49–70. *In* Baker, Robert J., J. Knox Jones, Jr., and Dilford C. Carter (eds.), Biology of bats of the New World family Phyllostomatidae. Part I. Special Pub. Mus. Texas Tech Univ., **10**:1–218.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy: The principles and practice of numerical classification. San Francisco, W. H. Freeman and Co., xv + 573 pp.

SOKAL, R. R., AND P. H. A. SNEATH. 1963. Principles of numerical taxonomy. San Francisco, W. H. Freeman and Co., xvi + 359 pp.

STANLEY, STEVEN M. 1973. An explanation for Cope's Rule. Evolution, 27:1–26.

START, ANTHONY N. 1969. A note on three species of bats (Chiroptera) not previously recorded from Kenya. Mammalia, 33:219–224.

STORCH, GERHARD. 1968. Funktionsmorphologische Untersuchungen an der Kaumuskulatur und an korrelieren Schädelstrukturen der Chiroptera. Abhandl. senckenberg. naturforsch. Ges., 571:1–92.

STORER, TRACY I. 1926. Bats, bat towers and mosquitoes. J. Mammal., 7:85–90.

STRUHSAKER, THOMAS T. 1961. Morphological factors regulating flight in bats. J. Mammal., 42:152–159.

TAMSITT, J. R. 1967. Niche and species diversity in neotropical bats. Nature, 213:784–786.

TAMSITT, J. R., DARIO VALDIVIESO, AND JORGE HERNANDEZ-COMACHO. 1964. Bats of the Bogota Savannah, Colombia, with notes on altitudinal distribution of neotropical bats. Rev. Biol. Trop., 12:107–115.

THOMAS, OLDFIELD. 1891. On the collection of small mammals made by Mr. F. J. Jackson in eastern Africa. Proc. Zool. Soc. London, 1891:181–187.

———. 1903. Three new species of Nyctinomus. Ann. Mag. Nat. Hist., ser 7, 12:501–505.

THOMPSON, D'ARCY W. 1971. On growth and form (edited by J. T. Bonner). New York, Cambridge University Press, xiv + 346 pp. + 2 pls.

TORRE, LUIS DE LA. 1956. The status of Mormopterus peruanus J. A. Allen. Proc. Biol. Soc. Washington, 69:187–188.

VALDIVIESO, DARIO, R. L. PETERSON, AND J. R. TAMSITT. 1979. Morphology of the basisphenoid pits and related structures of the bat Otomops martiensseni (Chiroptera: Molossidae). Life Sci. Contrib., Roy. Ontario Mus., 119:1–19.

VAUGHAN, TERRY A. 1959. Functional morphology of three bats: Eumops, Myotis, Macrotus. Univ. Kansas Publ., Mus. Nat. Hist., 12:1–153, 4 pls.

———. 1966. Morphology and flight characteristics of molossid bats. J. Mammal., 47:249–260.

———. 1972. Mammalogy. Philadelphia, W. B. Saunders Co., vii + 463 pp.

VERSCHUREN, JACQUES. 1957. Écologie, biologie et systématique des Cheiroptères. Explor. Parc. Nat'l. Garamba, Miss. de Saeger (ed.), Inst. Parcs Nat. Congo Belge, Brussels, 7:1–473.

VESTJENS, W. J. M., AND L. S. HALL. 1977. Stomach contents of forty-two species of bats from the Australasian Region. Australian Wildl. Res., 4:25–35.

WALKER, ERNEST P. 1975. Mammals of the world (3rd edition). Baltimore and London, The Johns Hopkins University Press, 2 vols., xvii + 1500 pp.

WARNER, JERRY W., JAMES L. PATTON, ALFRED L. GARDNER, AND ROBERT J. BAKER. 1974. Karyotypic analyses of twenty-one species of molossid bats (Molossidae: Chiroptera). Canadian J. Genet. Cytol., 16:165–176.

WHITAKER, JOHN O., AND RUSSELL E. MUMFORD. 1978. Foods and ectoparasites of bats from Kenya, East Africa. J. Mammal., 59:632–634.